

# **ABUNDANCE, DISTRIBUTION AND CONSERVATION VALUE OF SHARKS IN THE GALAPAGOS MARINE RESERVE**

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Chapters 2-4 of this thesis have been prepared as scientific manuscripts and will be submitted for review in the near future. In all cases, the experimental design, fieldwork, data analysis and interpretation, and manuscript preparation were the primary responsibility of the candidate. However, these studies were carried out in collaboration with supervisors and co-authors. Contributions of co-authors are outlined below:

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## Abstract

The Galapagos Marine Reserve (GMR) is the largest reserve in the Eastern Tropical Pacific (ETP), covering approximately 138000 km<sup>2</sup> of the pelagic environment surrounding the Galapagos Islands. The GMR hosts 33 species of sharks, of which two are endangered, four are near threatened, and eleven are vulnerable. In recognition of the importance of sharks to the reserve's marine ecosystem, a precautionary management framework was adopted to protect sharks from fishing and trading since 1989. Almost two decades have passed since the creation of the reserve, and yet knowledge on population levels and spatial use of the reserve by sharks is still limited. This information is critical to review the efficacy of the reserve in protecting mobile species and provide decision-supporting tools to improve shark management at the local and regional scale. The aim of this thesis was to assess and contrast the population status and habitat preferences of the endangered scalloped hammerhead shark (*Sphyrna lewini*) and other commonly occurring shark species in the GMR. Specifically, my work aimed to: *i*) assess the current population size of the scalloped hammerhead in the northern GMR; *ii*) compare the historical abundance trends of hammerhead sharks and five other common shark species; and, *iii*) assess the differences in spatial and temporal use of the GMR between the scalloped hammerhead shark and the coastal blacktip shark (*Carcharhinus limbatus*).

Whilst there are many techniques to evaluate the population size of wide-ranging terrestrial wildlife, constraints imposed by challenging underwater conditions have halted their wider application to evaluate wide-ranging marine species. To investigate the population size of hammerhead sharks I applied a novel mark-resight approach by combining acoustic telemetry and visual counts. During September 2011, September 2012, and October 2013 field trips deploying acoustic tags and

undertaking underwater visual surveys (USV) were conducted at Darwin Island, north GMR. Resident population ( $N^-$ ) and super-population ( $N^*$ ) size were modelled using the Immigration-Emigration Logic Normal Mark-Resight Estimator (IELNE) implemented in the Mark 8.0 software. Although the resighting probabilities based on acoustic detection were generally low (average 2011=0.25; 2012=0.19; 2013=0.16), I found strong evidence of time- and session-dependent resighting probabilities and individual heterogeneity in the resighting probability, particularly for 2012. Model estimations were less variable and with narrower confidence intervals for years 2011 ( $N^- \sim 487$  ind.;  $N^* \sim 590$ ) and 2013 ( $N^- \sim 391$  ind.;  $N^* \sim 574$ ), compared to 2012 ( $N^- \sim 642$  ind.;  $N^* \sim 1672$ ). Temporary emigration of marked and unmarked hammerheads affected estimations for some days in 2012, yet such emigrations become increasingly likely when assessing highly mobile species with gregarious behaviour. Despite this, my analysis provided a reliable approximation of the population size of hammerhead sharks in this ecological hot-spot, and gives support to the use of combined approaches in underwater mark-resight experiments. Further work should explore the inclusion of environmental covariates with increased numbers of tags to improve estimations of resighting probability and population size in case of temporary emigration of marked and unmarked individuals.

Abundance is commonly used to assess the status of wildlife populations and their responses to changes in management frameworks. Unfortunately, monitoring abundance trends often requires long-term data collection programs, which are not always carried out. One alternative to scientific surveys is to utilise local ecological knowledge (LEK) to evaluate abundance trends in data deficient regions. To assess the historical population trends of six shark species in the GMR, I developed a LEK-based virtual abundance change (VAC) model by using the ecological knowledge of

experienced divers. This model assessed the decadal deficit or surplus in shark abundance since the beginning of the dive tourism industry in the 1980s. In general, dive guides showed consensus on negative trends for all shark species, and suggested fisheries as the major factor driving trends in shark abundance in the GMR. VAC model results suggest that hammerhead and whitetip reef sharks (*Triaenodon obesus*) have experienced the most consistent perceived decline over the last four decades. Silky sharks (*C. falciformis*) and Galapagos sharks (*C. galapagensis*) also experienced perceived declines but later stabilized. Whale shark (*Rhincodon typus*) abundance was perceived as stable across the study time frame, while blacktip sharks were perceived to have increased in abundance in recent decades. Comparing the VAC results with empirical datasets from the GMR and the ETP provided corroborating evidence that the dive guides' ecological knowledge has described the abundance fluctuations of all species except silky sharks.

Spatial management through the implementation of marine protected areas (MPA) is one strategy to limit the extraction of commercial and/or sensitive species. Yet, its use to protect wide ranging marine predators is still unproven, mostly as their movements quite often exceed the established boundaries of MPAs. Understanding the area used by marine life is thus a key step towards the evaluation of the management framework and efficacy of a protected area. To provide information of the protective coverage of the GMR I assessed the habitat utilization distribution (UD) of hammerhead sharks and blacktip sharks in and around the GMR. My results show important aspects of the extent and seasonality of the UD of hammerhead sharks and blacktip sharks inhabiting the GMR. Nearly 90% of hammerhead shark's UD was enclosed by the reserve boundary during the cold season (June-October), yet this progressively decreased to only ~30% with the advent of the warm season

(December-April). Conversely, blacktip sharks' UD was 100% enclosed by the reserve boundaries in all seasons. Season and depth were the most important environmental parameters defining the core UD of hammerhead sharks; whilst year and eddy kinetic energy were the most important parameters for blacktip sharks. These findings suggest the size of the GMR may result in seasonally variable protective coverage for sharks inhabiting either pelagic or coastal-pelagic environments.

This study suggests that the current population size of the endangered scalloped hammerhead sharks within the GMR reflects only approximately 50% of the abundance seen four decades ago. The area used by this species exceeds the reserve size especially during the warmer months, making it vulnerable to fisheries operating around the reserve boundaries. While the GMR is providing important protective coverage for other species, arresting the decline of the scalloped hammerhead shark in the GMR may rely on revisiting the spatial management of fisheries beyond the reserve boundaries. The population assessment tools developed through this research could aid the future evaluation of the status of not only this but other wide-ranging species.

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## Chapter 1 *General introduction*

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### 1.1 General overview

Sharks are classified within the superorder Selachii, sub-class Elasmobranchii, class Chondrichthyes. They are a prehistoric group of fishes that evolved more than 400 million years ago ([Hickman et al. 2013](#)). Elasmobranchs (sharks and rays) are characterized by their cartilaginous skeleton, connective tissue, lack of a swim bladder, and jaws made of calcium crystals similar in strength to bones found in other vertebrates ([Compagno et al. 2005](#)). Sharks have between five to seven gills, but unlike bony fish the gill slits are uncovered ([Hickman et al. 2013](#)). Their skin is also distinctive from other fish classes. The surface of the skin is covered in dermal denticles also known as placoid scales ([Compagno et al. 2005](#)). These are arranged as helical networks, and promote faster swimming by reducing hydrodynamic drag ([Oeffner and Lauder 2012](#)).

At present, there are more than 500 extant species of sharks inhabiting a wide range of habitats around the world ([Eschmeyer and Fricke 2016](#)). Their range includes tropical freshwater riverine and lake systems (e.g. bull shark *Carcharhinus leucas*), coastal waters (e.g. zebra shark *Stegostoma fasciatum*), open seas (e.g. blue shark *Prionace glauca*), deep seas (e.g. sleeper shark *Somniosus pacificus*) and polar regions (e.g. Greenland sharks *Somniosus microcephalus*) ([Compagno et al. 2005](#)). Despite their worldwide distribution, most sharks and rays are restricted within these habitats ([Priede et al. 2006](#)). It is estimated that less than 5% of elasmobranchs occur in fresh water, approximately 5% are oceanic and highly migratory, 50% of elasmobranch species occur in coastal waters down to 200m in depth, 35% in deeper

waters down to 2000m, and 5% of species inhabiting more than one of these habitats ([Camhi et al. 1998](#)).

Sharks are generally long-lived, slow-growing species, reaching maturity at 75% of their maximum body size and produce few offspring over their lifetime ([Camhi et al. 1998](#)). The life span of sharks can vary between 3 years as seen in the spiny dog fish, *Squalus acanthia* ([Simpfendorfer 1993](#)) and up to 70 years as seen in whale sharks ([Hsu et al. 2014](#)); yet most sharks live between 20 to 30 years ([Camhi et al. 1998](#)). Sexual maturity is commonly reached between 5 to 15 years of age ([Cortés 2000](#)). As such, sharks' natural population rebuilding potential is amongst the lowest found in marine fish species ([Au et al. 2009](#); [Worm et al. 2013](#)).

Sharks are important components of marine ecosystems. Most sharks are at or near the top of marine trophic webs, exerting top-down regulatory control on the density and diversity of their prey species ([Stevens et al. 2000](#)). Sharks are also an important source of economic income for extractive and non-extractive activities. The worldwide trade of shark commodities is valued at approximately USD 1 billion per year ([Fischer et al. 2012](#)), whilst elasmobranch tourism is worth more than USD 315 million a year ([Cisneros-Montemayor et al. 2013](#)).

### **1.1 The collapse of shark populations**

The rapid expansion and development of fisheries is driving many elasmobranch species to severe population decline ([Ferretti et al. 2010](#)). It is estimated that between 63-273 million sharks are caught yearly at a rate that considerably surpasses their natural rebuilding potential ([Worm et al. 2013](#)). As such, approximately one quarter of the 1041 known shark and ray species are considered threatened ([Dulvy et al. 2014](#)). Issues regarding shark overfishing are being

increasingly discussed throughout the scientific literature. For example, trawl fisheries in the Mediterranean sea have led to the loss of 14 species of sharks from recorded catch compositions since the 1950s ([Aldebert 1997](#)). Pelagic fisheries landings in Brazil noted the disappearance of 14 species of carcharhinids ([Amorim et al. 1998](#)). Longline fisheries in the Gulf of Mexico led to the decline of the overall shark assemblage by 92 % between the 1950s and 1980s ([Baum and Myers 2004](#)). The resulting ecosystem restructure following the loss of these predatory species has also been reviewed, suggesting strong cascading effects in trophic webs affecting the overall ecosystem stability and resilience ([Worm et al. 2006](#)).

Efforts to reduce or halt shark population collapse have grown in the last decade as a result of increased public awareness of issues within shark fisheries, particularly pertaining to shark finning. The Food and Agricultural Organization (FAO) released a set of guidelines for responsible shark fisheries which were voluntarily implemented by many countries involved in shark fishing ([Fischer et al. 2012](#)). Although there have been several improvements in international and national regulations, these have not been sufficient to halt the global decline of shark populations ([Davidson et al. 2015](#)). One of the underlining reasons for this relates to how shark catches are managed. Sharks have often been caught as by-catch of fisheries targeting teleost fish species ([Barker and Schluessel 2005](#)). As such, shark composition and contribution to catches were long underreported ([Shotton 1999](#)), impeding the assessment of reliable catch statistics and demographic parameters to inform management decisions ([Clarke et al. 2006](#)). Without this information, regulation of fishing intensity has been based on the assessment of teleost fishes, which have productivity rates considerably exceeding those of shark species ([Au et al. 2009](#)).

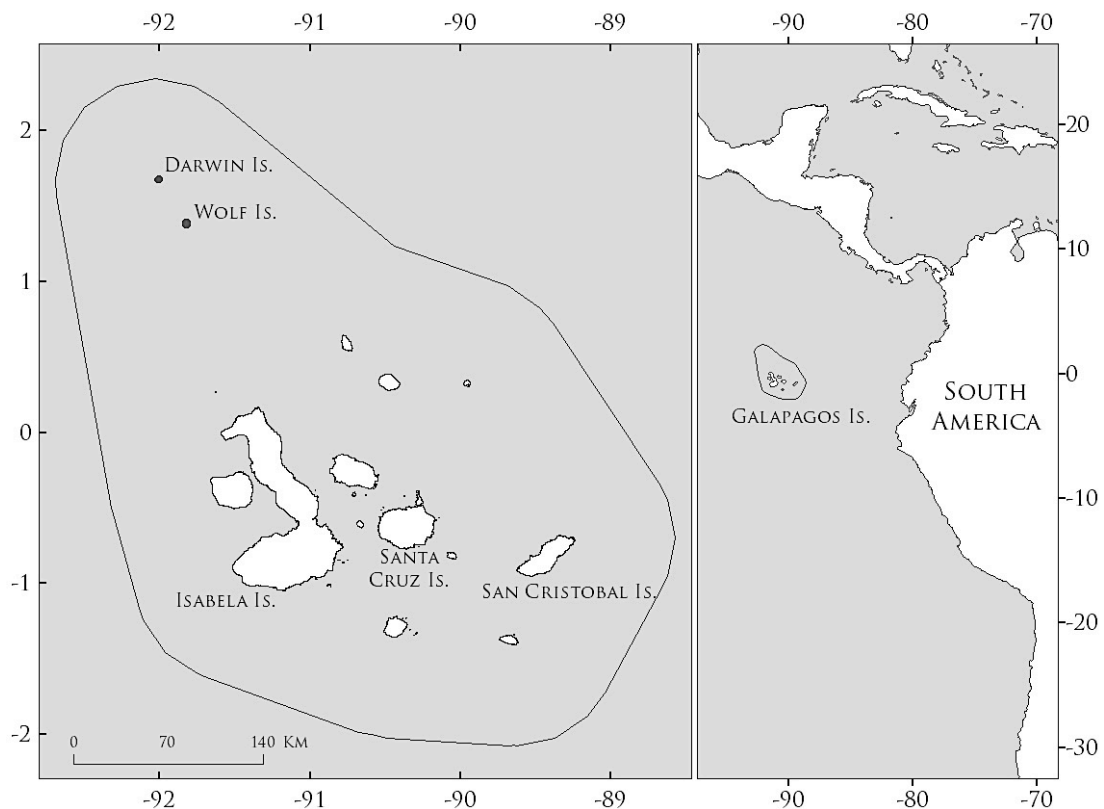
## 1.2 Management alternatives

To avoid the collapse of shark populations it is necessary to reduce fishing mortality below sharks' natural population rebound potential ([Worm et al. 2013](#)). Yet, achieving this goal is unpractical in open fishing grounds under the current fishing regimes ([Au et al. 2009](#)). Alternatively, the creation of spatial closures can limit the extraction of sharks and provide the tools to rebuild their populations ([Game et al. 2009](#); [Myers and Worm 2005](#)). There is substantial supporting evidence for the implementation of marine protected areas (MPA) to maintain and rebuild the biomass and diversity of coastal fish species (e.g. [Edgar et al. 2014](#); [Halpern 2003](#)), including sharks ([Friedlander and DeMartini 2002](#); [Robbins et al. 2006](#)). Overfished pelagic sharks could greatly benefit from the creation of MPAs, particularly if their reproductive and early life stages are encompassed by the reserves' boundaries ([Au et al. 2009](#)). Yet, MPA efficacy to protect highly mobile species is still a subject of debate among scientists (e.g. [Game et al. 2009](#); [Game et al. 2010](#); [Kaplan et al. 2010](#)). Wide-ranging marine predators such as sharks show extensive movements across a diversity of habitats often larger than most MPAs and national jurisdictions (e.g. [Abascal et al. 2011](#); [Domeier 2006](#); [Papastamatiou et al. 2013](#); [Sequeira et al. 2013](#)). Whilst several considerably large MPAs have been created in the last few decades, it is still unknown to what extent they are providing protection to shark populations ([Wood et al. 2008](#)). To support the wider implementation of MPAs and prevent shark population collapse and extinction, it is thus necessary to provide evidence of the effectiveness of those currently in place.



### 1.3 Marine protected areas: The Galapagos Marine Reserve case

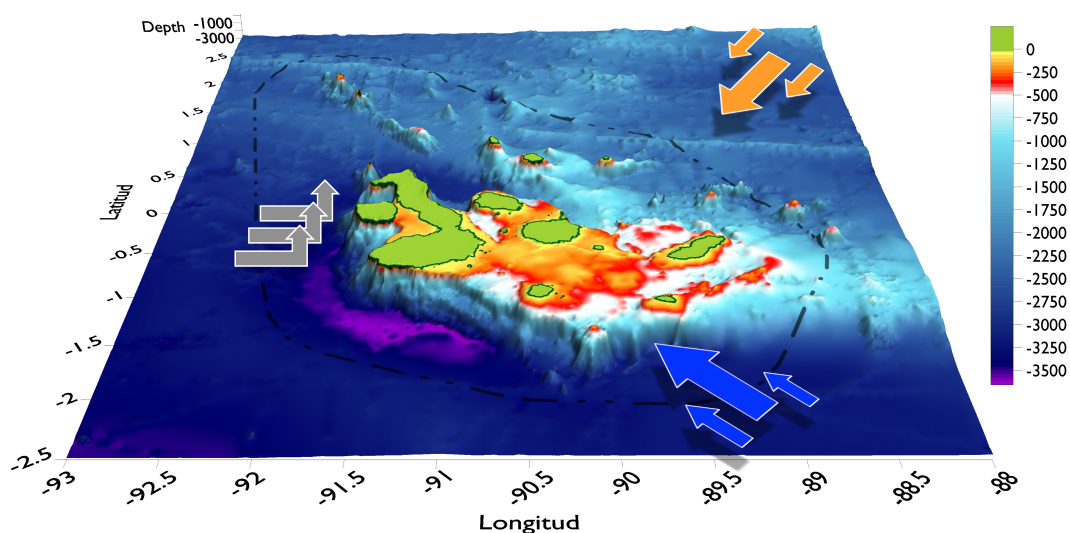
The Galapagos Marine Reserve (GMR) is located in the Eastern Tropical Pacific Ocean (ETP), approximately 1000 km east from the continental coast of Ecuador, South America (Figure 1.1). It is the largest MPA in the ETP, covering an area of approximately 138,000 km<sup>2</sup> (approximately 133,000 km<sup>2</sup> excluding island areas) ([Danulat and Edgar 2002](#)). The GMR encloses an archipelago consisting of 13 major islands, 6 minor islands, over 100 islets and emergent rocks, as well as shallow and deep seamounts ([Snell et al. 1996](#)). The islands form a shallow platform with depths between 0 to 1000 m, and are surrounded by steep cliffs up to 4000 m deep ([Geist and Harpp 2009](#)).



**Figure 1.1** Geographic location of the Galapagos Marine Reserve (GMR boundary: black line).

Waters within the GMR are affected by three major ocean current systems that shape the oceanographic conditions into two distinct seasons: the warm-water season, from

December to April; and the cold-water season, from June to October ([Figure 1.2; Houvenaghel 1984](#)). May and November represent the transition months between both seasons. The strengthening of the Panama current shapes the warm conditions in the archipelago, raising sea surface temperature (SST) to 25-30°C and decreasing the salinity to 30-34‰ around the reserve ([Banks 2002](#)). The cold season is driven by the Humboldt current, which lowers SST to 14–23°C and raises salinity to 35‰, especially in the south and central areas of the GMR ([Banks 2002](#)). The submerged Cromwell current does not affect the seasons, but its upwelling creates patches of high primary productivity in the west facing sides of Fernandina and Isabela islands, and in the central area of the archipelago ([Schaeffer et al. 2008](#)).



**Figure 1.2** Ocean current system affecting the GMR: Orange arrows, warm Panama Current; blue arrows, cold Humboldt Current; and, grey arrows, submerged Cromwell Current (GMR boundary: black dashed line). Coloured scale represents depth in meters.

### 1.3.1 GMR management

The first attempt to provide adequate management of the marine ecosystems in the Galapagos occurred in 1986 with the declaration of the Galapagos Marine Resources Reserve ([Gobierno del Ecuador 1986](#)). Unfortunately, it suffered from many legal

gaps and complex regulations that hampered its adoption and enforcement by the national authorities ([Altamirano and Aguiñaga 2002](#)). Shark-finning activities increased during this period, raising concerns for the sustainability of shark populations, that ended with the prohibition of shark fishing, trading and export within the Galapagos region ([SRP 1989](#)). While these efforts provided an important legal framework to protect sharks, it was only after the establishment of the GMR in 1998 that shark protection enforcement gained momentum ([Altamirano and Aguiñaga 2002](#)).

The creation of the GMR defined a 75 km boundary around the archipelago in which industrial fishing was prohibited and selected artisanal fishing gear (e.g. longlines) could not be used ([GNPS 1998](#); [Gobierno del Ecuador 1997, 1998](#)). The intent of the establishment of the GMR was to provide protection to the coastal ecosystem and to a significant proportion of the surrounding pelagic areas ([Danulat and Edgar 2002](#)). Yet, at the time there was no information available on the population state, spatial behaviour or habitat preferences of any highly mobile species that could inform the reserve design. As such, it is unknown how the reserve setting could have influenced the population trends of sharks and to what extent it provides protection.

### **1.3.2 GMR diversity and potential to rebuild shark-populations**

The GMR hosts an important number of shark species. Currently, there are 33 species known to inhabit the coastal, pelagic and deep sea ecosystems of the archipelago ([Hearn et al. 2014](#)) (Table 1.1). There are two species of high conservation concern: The scalloped hammerhead shark (*Sphyrna lewini*) and the great hammerhead shark (*S. mokarran*), both listed as endangered due to the large decline of their populations worldwide ([Baum et al. 2007](#); [Denham et al. 2007](#)). Eleven other shark species are

categorized as vulnerable. The majority are pelagic species, such as the thresher shark, oceanic shark, and whale shark, but the list also includes coastal species such as the spiny dogfish and hound shark.

**Table 1.1** Shark species reported from the Galapagos Islands. Source: [Hearn et al. \(2014\)](#); and [www.iucnredlist.org](http://www.iucnredlist.org).

No.	English name	Scientific name	IUCN red list
1	Pelagic thresher shark	<i>Alopias pelagicus</i>	Vulnerable
2	Bigeye thresher shark	<i>Alopias superciliosus</i>	Vulnerable
3	Long nose catshark	<i>Apristurus kampa</i>	Data deficient
4	Catshark	<i>Apristurus stenseni</i>	Data deficient
5	Galapagos catshark	<i>Bythaelurus giddingsi</i>	Not evaluated
6	Silvertip shark	<i>Carcharhinus albimarginatus</i>	Near threatened
7	Bignose shark	<i>Carcharhinus altimus</i>	Data deficient
8	Silky shark	<i>Carcharhinus falciformis</i>	Near threatened
9	Galapagos shark	<i>Carcharhinus galapagensis</i>	Near threatened
10	Blacktip shark	<i>Carcharhinus limbatus</i>	Near threatened
11	Oceanic whitetip shark	<i>Carcharhinus longimanus</i>	Vulnerable
12	Sandbar shark	<i>Carcharhinus plumbeus</i>	Vulnerable
13	White shark	<i>Carcharodon carcharias</i>	Vulnerable
14	Deep water spiny dogfish	<i>Centrophorus squamosus</i>	Vulnerable
15	Combtooth dogfish	<i>Centroscyllium nigrum</i>	Data deficient
16	Prickly shark	<i>Echinorhinus cookei</i>	Not evaluated
17	Catshark	<i>Galeus sp.</i>	Not evaluated
18	Tiger shark	<i>Galeocerdo cuvier</i>	Near threatened
19	Galapagos bullhead shark	<i>Heterodontus quoyi</i>	Data deficient
20	Cookie cutter shark	<i>Isistius brasiliensis</i>	Least concern
21	Shortfin mako shark	<i>Isurus oxyrinchus</i>	Vulnerable
22	White-margin fin smooth-hound shark	<i>Mustelus albipinnis</i>	Data deficient
23	Speckled smooth-hound	<i>Mustelus mento</i>	Near threatened
24	White nose shark	<i>Nasolamia velox</i>	Data deficient
25	Smalltooth sand tiger shark	<i>Odontaspis ferox</i>	Vulnerable
26	Blue shark	<i>Prionace glauca</i>	Near threatened
27	Whale shark	<i>Rhincodon typus</i>	Vulnerable
28	Scalloped hammerhead shark	<i>Sphyrna lewini</i>	Endangered
29	Great hammerhead shark	<i>Sphyrna mokarran</i>	Endangered
30	Bonnethead shark	<i>Sphyrna tiburo</i>	Not evaluated
31	Smooth hammerhead shark	<i>Sphyrna zygaena</i>	Vulnerable
32	Whitetip reef shark	<i>Triaenodon obesus</i>	Near threatened
33	Spotted hound shark	<i>Triakis maculata</i>	Vulnerable

The scalloped hammerhead is a coastal-pelagic shark species inhabiting warm temperate and tropical seas across the world ([Compagno et al. 2005](#)). Despite its broad distribution, important genetic differences can be found among neighbouring oceanic regions ([Duncan et al. 2006](#)), which makes it highly vulnerable to localized extractive activities. In the Galapagos, this species is observed aggregating in relatively large schools across the reserve but particularly around the northern islands of Darwin and Wolf ([Hearn et al. 2014](#)). It is regarded as one of the most charismatic species due to its peculiar body shape and relatively high abundance ([Hearn et al. 2014](#); [Peñaherrera et al. 2013](#)). Efforts to understand their behaviour around oceanic islands of the GMR have provided important information on the fine scale movement and site fidelity of this species ([Ketchum et al. 2014a](#); [Ketchum et al. 2014b](#)). Yet, it is still unknown how hammerhead and other shark species use the reserve on a larger scale.

The potential of the GMR to provide a safe ground for sharks to maintain or rebuild their population has been subject to debate. Anecdotal evidence by dive guides suggested the abundance of shark species, including hammerhead sharks, have considerably declined at the main dive sites since the 1990s ([Zarate 2002](#)). Yet, [Wolff et al. \(2012a\)](#) recently proposed that the occurrence of the El Niño event in 1997-1998, along with the creation of the reserve in 1998, provided the ideal scenario in which several shark species could have increased their biomass. Theoretical population increases of 37% were suggested for coastal-pelagic sharks, 24% for large pelagic sharks, and 15% for hammerheads sharks. Also, biomass increase in large predators was modelled to induce a 20% decline in the biomass of small-sized sharks. While [Wolff et al. \(2012a\)](#)'s findings were modelled under scenarios of reduced illegal harvesting, there are concerns that the intensity of shark poaching could have been

maintained at the level previous to the reserve setting ([Schiller et al. 2014](#)). Marked fishing pressure around the border of the reserve ([Martinez-Ortiz et al. 2015](#)) and constant seizure of poachers inside the reserve ([Carr et al. 2013](#); [Reyes and Murillo 2007](#)) support these concerns. To date, there is no available information on shark population size and trends that could aid the evaluation of the protective coverage of the GMR to shark species.

#### **1.4 Project motivation and objectives**

Unprotected seas around the world provide no safe haven for shark populations under current fishing regimes. The size and management of the GMR could provide a safe ground for sharks whilst playing a key role in buffering the current decline of shark populations observed across the ETP. This doctoral research program uses the endangered scalloped hammerhead shark as a study case to assess the GMRs efficacy in protecting pelagic sharks. The scalloped hammerhead is still found in large aggregations in the GMR, providing a unique opportunity to examine the benefits of MPAs for this species. Moreover, the GMR can be considered one of the few places where marine communities are still diverse and abundant ([Edgar et al. 2014](#); [Stuart-Smith et al. 2013](#)); knowledge from such study sites is invaluable in the face of the current rate of extinction and habitat degradation facing marine ecosystems worldwide.

The thesis is divided into five sections: an introduction, three main data chapters and a discussion chapter. The introductory chapter reviews the issues of shark fisheries, the management framework and biological baseline data on which shark management in the Galapagos Marine Reserve is based upon. The first data chapter (chapter 2) assesses the feasibility of using acoustic telemetry-visual surveys

combined with mark-resight approaches to provide estimations of the population size of the scalloped hammerhead shark in an oceanic hot-spot. The second data chapter (Chapter 3) explores the historical trends in abundance of six shark species by evaluating the local ecological knowledge of dive guides working in the Galapagos since the beginning of the tourism industry. The third data chapter (Chapter 4) aims to evaluate and compare the movement, home range and environmental preferences of the scalloped hammerhead shark to the coastal blacktip shark. My concluding chapter (General Discussion, Chapter 5) explores the use of the tools developed through this research thesis and the available information to inform scientists, stakeholders and managers on the protective effect of the GMR for the conservation of sharks, in particular the scalloped hammerhead.

The objectives of my research are closely aligned to the Ecuadorean National Plan of Action for Sharks, the International Plan of Action for Sharks, and the Galapagos Marine Reserve Management Plan. This work aims to highlight and provide essential information regarding historical and current shark abundance, how sharks use the reserve, and their preferred environmental conditions. This information was primarily obtained to aid scientists and GMR managers to make informed decisions towards improving the management framework in the Galapagos.

This project is part of a multi-institutional effort in collaboration with the University of Tasmania (UTAS), the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Directorate of the Galapagos National Park (DGNP), The Charles Darwin Foundation (CDF), The University of California - Davis, Turtle Island Restoration Network (TIRN) and OCEARCH.

## **Chapter 2** *Short-term fluctuations in hammerhead shark numbers at an aggregation site based on visual census and telemetry data*

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### **2.1 Abstract**

The application of mark-resight experiments in marine science has been sparse due to constraints imposed by challenging underwater conditions, particularly in relation to the visual sighting of marked individuals. The recent development of more general mark-resight estimators provides the framework to test the use of alternatives to sighting methodologies, such as acoustic telemetry. Here I explored the use of acoustic telemetry in combination with underwater visual surveys (UVS) to assess the population size of the endangered scalloped hammerhead shark. During September 2011, September 2012, and October 2013 field trips deploying acoustic tags and conducting UVS were carried out at Darwin Island, Galapagos Marine Reserve. Resident population and super-population size were modelled using the Immigration-Emigration Logic Normal Mark-Resight Estimator (IELNE). In 2011, the estimations of super-population size (average 605 ind.) were approximately 1.2 times larger than the resident population size (average 499 ind.). Estimations for year 2012 produced the largest values of super-population size in this study (average 1739 ind.), almost 2.6 times the resident population size (average 665 ind.). In 2013, the estimations of super-population size (average 588 ind.) were on average 1.5 times larger than the resident population size (average 401 ind.). Model estimations were less variable and with narrower confidence intervals for years 2011 (10 acoustic tags) and 2013 (20 tags), but not for 2012 (21 tags). The temporary emigration of marked and unmarked hammerheads affected estimations for some days in 2012. This scenario becomes increasingly likely when assessing highly mobile species with



gregarious behaviour. Despite this, my analysis produced a reliable approximation of the population size of hammerhead sharks in this ecological hot-spot. These results give support to the use of combined approaches in underwater mark-resight experiments, especially in areas where more traditional assessment techniques based on fishing are not appropriate.

## **2.2 Introduction**

Mark-resight methods are used to estimate the size of animal populations from sightings rather than physical recaptures of marked individuals ([Neal et al. 1993](#)). These methods only require a single “marking” event, without incorporating new marks during subsequent resighting periods. Abundance is estimated by incorporating sightings of unmarked individuals into the estimation framework. This contrasts with traditional mark-recapture, which relies on the post-tagging capture of individuals to identify the marks ([Cooch and White 2014](#)). Therefore, mark-resight routines allow a less invasive and potentially more cost-effective alternative to mark-recapture, and are especially useful when the physical recapture of individuals is challenging or imposes stress on sensitive species ([Minta and Mangel 1989](#)).

Mark-resight methods were primarily developed to assess the abundance of wide-ranging terrestrial fauna by means of visual observation or assisted with radio telemetry ([White and Garrot 1990](#)). These methods have been widely applied to assess species across a range of animal taxa, including bears ([e.g. Keech et al. 2014](#)), deer ([e.g. Bartmann et al. 1987](#)), prairie dogs ([e.g. McClintock et al. 2009](#)), raccoons ([Sollmann et al. 2012](#)), lions ([Castley et al. 2002](#)), sheep ([e.g. Neal et al. 1993](#)) and birds ([e.g. Dennhardt et al. 2015](#)). However, their application in marine science has been limited due to the difficulty of properly identifying marks in the marine domain.

Currently, the most common approach to resight marks rely on the visual identification of implanted marks ([conventional tags, e.g. Griffing et al. 2014](#)) or unique body markings ([photo-indentification, e.g. Mansur et al. 2012](#)). While this can be suitable to assess marine mammals that constantly surface to breathe ([Mansur et al. 2012](#); [Ryan et al. 2011](#)), the underwater identification of marks can be affected by poor visibility conditions, the animal depth, distance, and movement in relation to observers ([Seber 1992](#); [Zeller and Russ 2000](#)). Failure to account for marked individuals can directly affect the estimations of sighting probability, which constitutes the most important factor in mark resight experiments ([Neal et al. 1993](#)).

Acoustic telemetry is the use of sound to monitor the underwater presence of animals to known hydrophone locations ([Grothues 2009](#)). It has become an increasingly popular research tool in marine sciences due to its accuracy in producing reliable detection profiles of individuals in challenging underwater conditions ([Heupel et al. 2006](#)). This allowed its effective incorporation into traditional mark-recapture models for the estimation of natural mortality ([e.g. Heupel and Simpfendorfer 2002](#)), fishing mortality ([e.g. Pollock et al. 2004](#)), apparent survival ([e.g. Barbour et al. 2013](#)) and population size ([e.g. Dudgeon et al. 2015](#)). Mark-resight experiments could also benefit from the use of acoustic telemetry in sampling design. [Lee et al. \(2014\)](#) reported that estimations of abundance from telemetry-aided mark-resight experiments could produce similar abundance estimations (and with narrower confidence intervals) than Pollock's mark-recapture robust design ([Pollock 1982](#)) through photo-identification. [Lee et al. \(2014\)](#) study provided the first revision on the potential use of acoustic telemetry in underwater mark-resight experiments, yet they only used telemetry to determine the number of marked individuals in and out the study area prior to visual resighting events. Their approach is feasible for species that

spend prolonged periods of time resting on the sea floor, but becomes less practical with more mobile species such as coastal-pelagic sharks.

The scalloped hammerhead shark, *Sphyrna lewini*, is a coastal-pelagic shark species that has cryptic coloration with no individually identifiable body markings ([Compagno et al. 2005](#)). This species is known to display characteristic gregarious behaviour while constantly circumnavigating oceanic islands and seamounts ([Klimley and Oerding 2013](#)). Populations of hammerhead sharks are globally endangered as a result of targeted and by-catch overfishing ([Baum et al. 2007](#)). Hammerhead sharks have one of the highest reported mortality rates to hooking for a shark species ([Gulak et al. 2015](#)), making them highly susceptible to fisheries and any other activity that involves capturing individuals. The development of cost-effective and capture-independent assessment tools is critical to provide reliable estimations of population size while reducing the negative impacts associated with re-capturing individuals ([McClintock and White 2012](#)).

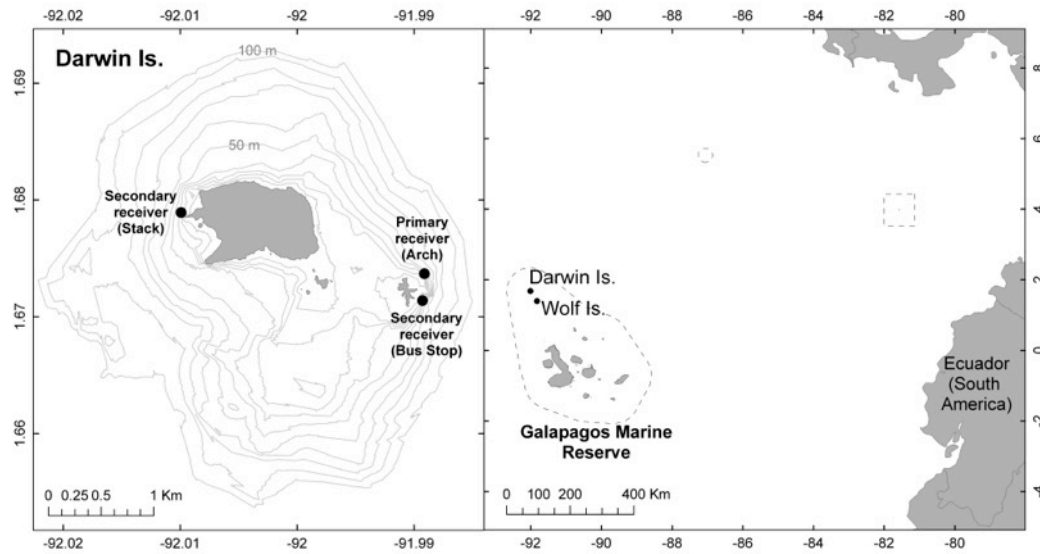
Here I explore the use of acoustic telemetry in combination with underwater visual surveys (UVS) to carry out mark-resight experiments and assess population size for the scalloped hammerhead shark in an ocean hotspot. Specifically, my work is designed to 1) construct encounter histories of a mark resight estimator using the acoustic-telemetry detection profiles of marked individuals; 2) provide estimations of local population sizes of the scalloped hammerhead; and 3) evaluate the model sensitivity to over and under counting bias associated to the combined use of UVS and acoustic telemetry. This species' characteristic schooling and residence behaviour at seamounts and oceanic islands provide a unique opportunity to test this approach and evaluate its effectiveness in assessing the population size of similar fish species.

## 2.3 Methods

### 2.3.1 Data collection

Field trips were carried out during September 2011, September 2012, and October 2013 at Darwin Island, the northern-most oceanic island in the Galapagos Marine Reserve (GMR). The GMR is the largest marine protected area in the Eastern Tropical Pacific where industrial fishing is banned and sharks are protected from all fishing, including local small-scale fisheries (Figure 2.1). I acoustically tagged sharks and conducted UVS at Darwin's Arch, which is a known aggregation hot-spot for hammerhead sharks ([Hearn et al. 2014](#)). I tagged sharks over the morning and afternoon of the first two days of every fieldtrip, followed by five to eight days of simultaneous UVS and passive acoustic tracking.

I fitted 10 (September 2011), 21 (September 2012) and 20 (October 2013) sharks with coded Vemco V16-6H tags (frequency 69 kHz, 160dB, nominal delay 90–180 s, diameter 16mm, length 95mm) tethered to a stainless steel dart with stainless steel wire. Tags were attached externally into the musculature behind the dorsal fin by using a pole spear while free diving. Tagging was carried out over the reef area at depths not greater than 15 meters. I placed one primary acoustic receiver in the Arch and two secondary receivers in nearby areas to track presence and movements of the tagged sharks around the island (Figure 2.1). I used Vemco VR2W (69 kHz) receivers set at 30 m deep and anchored to concrete blocks by PVC coated marine stainless steel cable ropes. The detection range of the primary receiver was estimated as 150 m, while the secondary receivers varied from 200 to 300 m ([for more technical details see Hearn et al. 2010](#)).



**Figure 2.1** *Left:* Location of the Arch (main study site) and receivers (black dots) placed around Darwin Is. *Right:* The location of the Galapagos Marine Reserve in relation to South America.

Following acoustic tagging, I carried out an UVS to collect the raw counts (hereafter called raw abundance), sex and size structure of hammerhead sharks around the primary receiver. UVS were carried out the next following day after tagging to avoid the risk of tag lost due to permanent emigration or mortality. A pair of divers carried out 20-minute UVSs three times per day: morning (between 07:00am to 10:00am), midday (10:30am to 14:00pm) and afternoon (14:00pm to 17:00pm). Number of sharks and their sex were counted by one diver, whilst the other collected data on sharks' fork length using laser photogrammetry equipment ([for equipment specifications and limitations see Rohner et al. 2011](#)). Only pictures in which I could clearly identify laser dots and the shark's body in a straight and perpendicular position to the camera were used to photogrammetrically measure length. Shark fork length was then converted into total length (TL) following [Branstetter \(1987\)](#). Divers remained in the vicinity of the acoustic receiver at depths between 20 to 40 meters. To ensure all sharks were counted when large aggregations passed by, divers swam out of the reef toward the open ocean to be as close as possible to the school without

disrupting sharks' normal behaviour. This sampling procedure allowed divers to extend their visual range up to 30 m away from the receiver.

Tagging and UVS protocols were approved by the University of Tasmania Animal Ethics Committee (permit No. A13641), by the Institutional Animal Care and Use Committee of the University of California – Davis (permit number IACUC PROTOCOL #16022), and by the Directorate of the Galapagos National Park (research permit No. PC-60-13).

### **2.3.2 Model construction**

I modelled population size using the Immigration–Emigration Logit-Normal Estimator (IELNE) implemented in the MARK 8.0 software ([Cooch and White 2014](#)). IELNE is a mark-resight modelling framework that does not require geographic closure ([McClintock and White 2012](#)). I built my IELNE models under Pollock's robust design framework, which combines secondary sampling occasions embedded in primary intervals ([Kendall 2001](#); [Pollock 1982](#)). I defined each UVS as a secondary occasion and each day (from 0:00 to 23:59) as a primary occasion. This produced three secondary sampling occasions for each primary occasion, and between five to eight primary occasions depending on the year. I used the presence of marked sharks (from acoustic telemetry) and raw abundance (from UVS) to construct the marked individual encounter histories for IELNE. For purposes of abundance estimation, I defined residents as individuals that were registered on a regular basis at the primary receiver with absences no greater than 24 hours. Individuals not detected for more than 24 hours were categorized as non-residents, following [Soria et al. \(2009\)](#) and [Capello et al. \(2015\)](#). Based on these definitions, encounter histories of resident marked individuals were assigned a "1" if they were acoustically detected at the Arch

(primary receiver) within the period of the 20 minute UVS survey, and “0” if otherwise. I considered the non-resident marked sharks as unavailable for sighting during UVS, and were thus assigned a “.” in the analysis matrix. The total number of marks deployed during each fieldtrip was registered as the marked super-population group (i.e., the number of tagged sharks using the study area), whilst the differences between the number of sharks counted per dive and the number of acoustically detected sharks in the corresponding UVS were considered the unmarked counts for each secondary sampling occasion.

IELNE models estimate two types of abundance: the mean population size ( $N_j$ ), and the super-population size ( $N^*_j$ ). Based on my study methods and design, the mean population size is the number of resident sharks in the primary receiver’s detection range during each primary period  $j$ ; while the super-population refers to the number of resident sharks using the entire Darwin Island receiver detection range and surrounding waters outside of the receivers area during each primary period  $j$ . Other output parameters obtained through this model are the mean re-sighting probability ( $p_{ij}$ ) for resident sharks within the receivers’ detection range during a secondary occasion  $i$  (i.e., the probability that a resident animal is within the Darwin Arch receiver range during a specific UVS); the overall mean resighting probability ( $\hat{u}$ ) for secondary occasion  $i$  of primary interval  $j$ ; the difference ( $\alpha_{ij}$ ) between the population size within the primary receiver’s detection range during a secondary occasion  $i$  of primary interval  $j$  and the mean population size during primary interval  $j$  (i.e.,  $\alpha_{ij} = N_{ij} - N_j$ ); and the individual heterogeneity level ( $\sigma^2_j$ ) in mean resighting probability during primary interval  $j$  (McClintock and White 2012). Candidate models were constructed by allowing parameters  $p_{ij}$ ,  $\sigma^2_j$ ,  $N_j$  and  $N^*_j$  to fluctuate either through only secondary occasions (time-dependent); only primary occasions (session dependent);

or to be constant across the whole fieldtrip. Initial parameter values estimated from the simplest time-independent model using the logit-link function were provided for each model in order to reduce potential convergence issues ([Cooch and White 2014](#)). Model selection criteria were based on the adjusted Akaike's Information Criterion (AIC) values to take into account differences in effective sample size and lack of fit ([Burnham and Anderson 2002](#)). Finally, I used parametric ([Analysis of Variance, Fisher 1918; Student's t-test, Student 1908](#)), and non-parametric ([Kruskal-Wallis test, Kruskal and Wallis 1952](#)) statistical analyses to test differences between the collected data, model estimates and between years and time of day.

### **2.3.3 Model assumptions and estimations**

For realistic estimations, my experimental design must fulfil at least four critical IELNE requirements: *i)* marks cannot be lost, *ii)* the number of marks available for resighting must be known during each occasion; *iii)* every sampling must be without replacement; and *iv)* the subset of the population selected for marking must be representative of the entire population in terms of sighting probability ([McClintock and White 2012](#)). While the presence of all marked sharks during and after their sampling sessions confirmed I fully met the first two assumptions, the telemetry-based approach may not completely fulfil the last two requirements. Hammerhead sharks do not have distinctive natural body markings that allow divers to accurately identify individuals and avoid re-counting individuals. This increases the risk of overestimating the real raw abundance of sharks swimming by the study site (violation of assumption *iii*). Moreover, the combination of acoustic telemetry and USV represents a risk of not observing individuals swimming out of the divers' visual



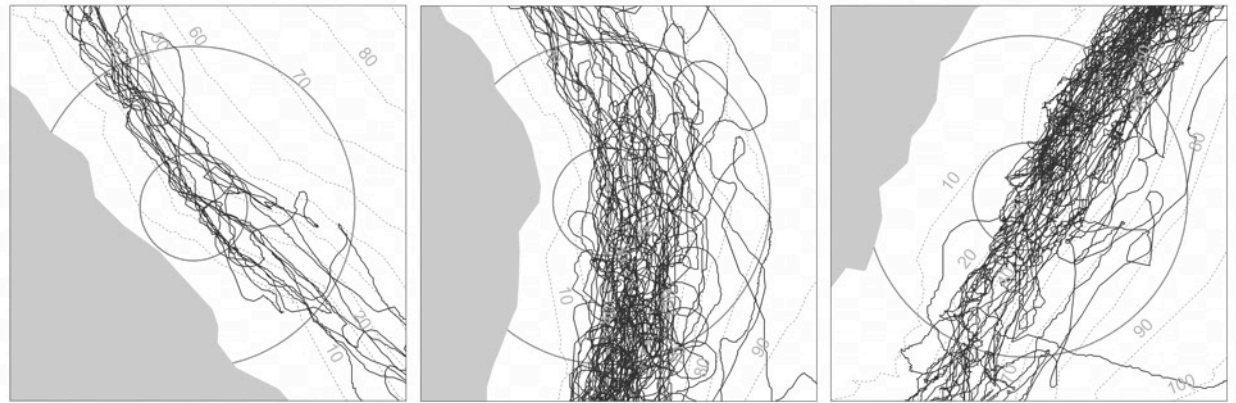
range (30 m) yet within the acoustic detection range (150 m), potentially resulting in underestimations of the collected raw abundances (violation of assumption *iv*).

To evaluate the effect of violating these assumptions and correct my data from both sources of bias, I used passive and active acoustic telemetry data to estimate a replacement and a difference in sighting probability (hereafter availability) ratio. Replacement and availability were modelled on the assumption that both scenarios are directly associated with the entries and departures of sharks to and from the study site. The replacement ratio was calculated using the acoustic detections profiles of all marked sharks during my surveys. To achieve this, I binned (in 5 min intervals) all the detections collected during daytime hours (6 am to 6pm) at the primary receiver and for each shark separately, and performed a sliding selection of every possible 20 min timeframe that could have recorded a marked shark at least once. This represented my total number of possible UVS within a day. Following [Melnychuk and Walters \(2010\)](#), I counted all the potential replacement events in which a marked shark would display an entry – re-entry detection pattern across a fixed acoustic receiver. The final replacement ratio was then calculated as the mean product of the possible replacement events over all possible UVS. The availability ratio was calculated using the fine-scale movement data for hammerhead sharks collected at Wolf Island ([full details in Ketchum et al. 2014a](#)), given there is not an equivalent dataset available for Darwin Island. I selected the dataset of sharks actively tracked during the cold season (July-November) and over three sites (East Bay, Shark Point, and Rockfall, Figure 2.2) that share similar biophysical conditions and high hammerhead shark connectivity with my study site than with any other area of the GMR ([Hearn et al. 2010](#); [Ketchum et al. 2014b](#)). Following [Dennhardt et al. \(2015\)](#), I used the Tracking Analysis tool available in the ESRI ArcGIS 9.3 software, and

calculated the availability ratio as the number of times a shark entered only within the detection range area (excluding the visual range) over the total number of times it entered the entire detection range area (including the visual range). The resulting replacement and availability ratios were used to correct my raw abundance with the following equation:

$$A_{Ci} = (1 - S) * A_i / (1 - R) \quad (1)$$

Where  $A_{Ci}$  represents the corrected raw abundance for secondary occasion  $i$ ,  $A_i$  is the measured raw abundance for secondary occasion  $i$ ,  $S$  is the availability ratio, and  $R$  the replacement ratio. IELNE models were constructed using the corrected raw abundances for every year.



**Figure 2.2** Movement of continuously tracked hammerhead sharks superimposed on the receiver's detection range (*external black circle – 150m radius*) and diver visual range (*inner black circle – 30m radius*) over the site East Bay (*left*), Shark Point (*centre*) and Rockfall (*right*) sites from Wolf Island ([From Ketchum et al. 2014a](#)).

To further understand the effect of violating model assumptions (iii and iv) several models were simulated to test the effect of under- and over-counting the raw abundance in the estimations of mean population and super-population size. By varying the uncorrected raw abundances in both reductions and increases of 5%, 10%, 15% and 20%, I re-estimated the population size using the most parsimonious

model for each year. I used the percentage of relative bias (PRB), the main percentage of confidence interval length (PCIL) and CI coverage indicators to compare the results obtained from these simulations with those of the basic models of “no variation” in uncorrected raw abundances ([for more technical information on these indicators see Neal et al. 1993](#)).

## **2.4 Results**

### **2.4.1 Sampling conditions**

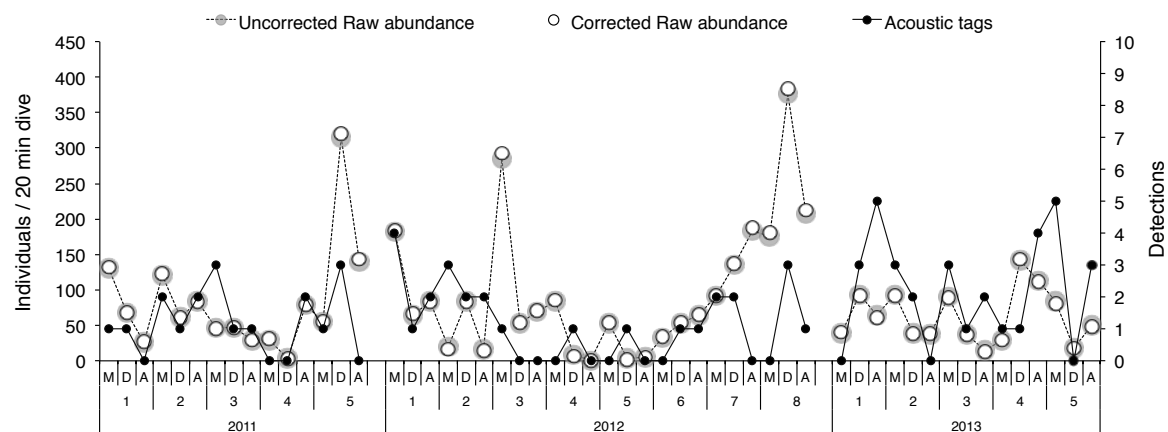
A total of fifty-one sharks were acoustically tagged (marked) over three years (Table 2.1). All, except one shark (tagged in 2011) were detected during subsequent sampling days. The undetected shark moved out of the study area immediately after being tagged, but was detected one month later by an acoustic receiver located at Wolf Island, showing emigration rather than tag loss. In 2011 significantly smaller sharks were marked (mean=218.2 cm, Kruskal-Wallis  $X^2=17.9713$ ,  $p=0.001$ ) and observed (mean=229 cm, 49 ind.; Kruskal-Wallis  $X^2=6.2314$ ,  $p=0.044$ ) compared to 2012 and 2013. The largest and broadest body size spectra were marked in 2013 (mean =242.9 cm; min=195, max=286), followed by 2012 (mean =235.3 cm; min=221, max=260). The largest and broader observed size spectra were recorded for year 2012 (242.3 cm), followed by 2013 (237 cm). I found no significant differences between the mean total length of the marked and observed sharks within year, with exception of the year 2011 when marked sharks were slightly smaller than those measured through UVS (t-test  $t=2.2512$ ,  $p=0.03$ ). I could not identify the sex of the marked sharks due to the angle of the free diver while tagging the individuals. Female hammerheads from UVS accounted for 84 to 89% of the observed schools sex

composition, with no significant differences between years (two-way ANOVA year\*sex:  $F=0.1$ ,  $p=0.75$ ).

**Table 2.1** Sampling conditions of the acoustic telemetry and underwater visual surveys (UVS). *Raw Abun.* refers to the counted raw abundance (Ind./20 min dive) during UVS; Size is measured in cm.

Year	Marked sharks	Acoustic tagging					UVS			Sex composition (%)	
		Size	Marks detected during UVS			Day <sup>s</sup>	Raw Abun.	Size	Num	F	M
		Mean (SD)	2011	2012	2013		Mean (SD)	Mean (SD)			
2011	10	218.2 (11.9)	9	1	0	5	82 (75.7)	229.9 (24.9)	49	89	11
2012	21	235.3 (12.5)	---	21	0	8	97 (95.2)	242.3 (9.0)	48	84	16
2013	20	242.9 (21.1)	---	---	20	5	62 (37.4)	237.0 (23.4)	35	88	12

The counted raw abundance of sharks varied around a general mean of 83 ind./20 min across years, with peaks of abundance reaching up to 377 ind./20 min (Figure 2.3). Year 2012 had the highest mean raw abundance (97 ind./20 min) in comparison to year 2011 (82 ind./20 min) and 2013 (63 ind./20min; Table 2.1), yet differences in the raw abundance across years were not significant (Kruskal-Wallis  $X^2=0.43$ ,  $p=0.80$ ). The maximum raw abundance recorded in a single dive was 377 ind./20 min, and the lowest was zero. The raw abundance recorded in 2011 showed a peak of 315 ind./20 min, but a minimum of 4 ind./20 min. The least variable year was 2013, with only subtler changes across the five sampling days in comparison to previous years, yet the raw abundance varied from a minimum of 15 to a maximum of 141 ind./20 min. The average of morning (91 ind./20 min) and midday UVS (90 ind./20 min) were higher than the afternoon UVS counts (70 ind./20 min) but differences were not significant (Kruskal-Wallis  $X^2=1.34$ ,  $p=0.512$ ).



**Figure 2.3** Variation in hammerhead sharks uncorrected and corrected-raw abundance through UVS (left vertical axis) and the number of detected individuals at the main ultrasonic receiver (right vertical axis) during the three field trips. Horizontal axis refers to the days and time of dive (M, morning, D, midday; and A, afternoon).

The replacement ratio was relatively consistent across years (Table 2.2). The highest value was estimated for the fifth primary occasion in year 2012, coinciding with the lowest counted raw abundances of this study. The lowest values were also estimated for the same year, yet these were not related to any pattern in the amount of detected sharks of the counted raw abundance. Given that I found no significant differences between the estimated values between days and years (Kruskall-Wallis  $p>0.05$ ), I used the overall mean replacement (0.24) as the replacement ratio value ( $R$ ) in equation 1. In terms of the availability ratio (detected but unseen), movement analysis showed the majority of shark passes (0.74) occurred over both the detection and visual ranges (Figure 2.2). The remaining ratio (0.26) reflected sharks passing only over the detection range (remaining unseen by divers), and was used as my availability ratio  $S$  in equation 1. Final corrected raw abundances varied slightly (increment of 2%) from those measured (Figure 2.3). I found no significant

differences between the yearly means of the counted and corrected raw abundances (Anova 2011  $p=0.97$ ; 2012,  $p=0.96$ ; 2013,  $p=0.96$ ).

**Table 2.2** Daily mean of the replacement ratio estimated from the marked sharks.

	2011	2012	2013
Day 1	0.33	0.24	0.20
Day 2	0.21	0.22	0.21
Day 3	0.27	0.16	0.31
Day 4	0.23	0.17	0.31
Day 5	0.20	0.40	0.26
Day 6		0.18	
Day 7		0.23	
Day 8		0.18	
Mean	0.24	0.23	0.26
SD	0.11	0.13	0.13

The number of marked individuals detected within each UVS varied similarly to the (measured) raw abundance (Figure 2.3). While there were slightly more sharks detected during 2013 and during morning UVS, no significant differences were found between years (Kruskal-Wallis  $X^2=4.56$ ,  $p=0.102$ ) or time of day (Kruskal-Wallis  $X^2=0.22$ ,  $p=0.894$ ). Situations in which no shark was detected were also observed, particularly in year 2012 when nine UVS detected no sharks. These situations were often related to observed declines in raw abundances, especially during the second quarter of year 2012.

#### 2.4.2 Parameter estimations

I ran up to nine models for every yearly session from 2011 to 2013 (Table 2.3). Models with time- and session-dependent parameterizations for mean re-sighting rate ( $p$ ), and session-dependant values for the mean population ( $N^-$ ) and super-population size ( $N^*$ ) had the most support (e.g. lowest AIC values). Individual heterogeneity ( $\sigma^2$ ) was parameterized separately for each year, with the most

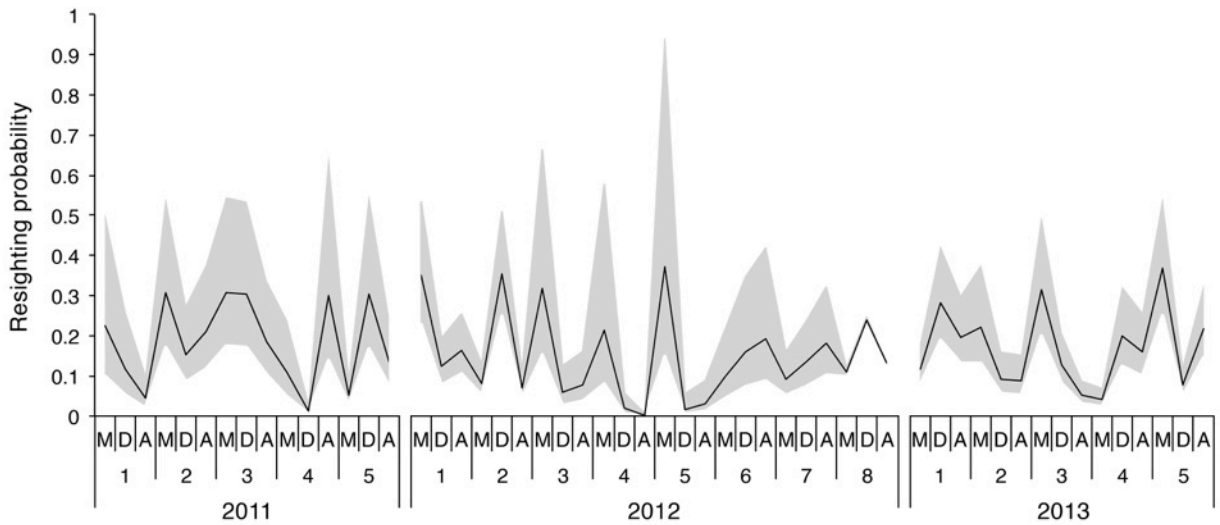
parsimonious 2011 model favoured by a constant  $\sigma^2$ , 2012 by session-dependent  $\sigma^2$ , and 2013 by a zero heterogeneity parameterization ( $\sigma^2=0$ ). For the first two years, the estimated values of  $\sigma^2$  were generally greater than 1 and provided some evidence of heterogeneity in the resighting probability, particularly for 2012.

**Table 2.3** AIC weights for selected IELNE models based on the corrected raw abundances of scalloped hammerhead shark abundance at Arch of Darwin Island. Only top-five models are shown in this table.

Model	AICc	Delta AICc	AICc Weights	Num. Par.
2011				
$p(session*t) \sigma(.) N^-(session) N^*(session)$	260.82	0	0.6142	25
$p(session*t) \sigma(0) N^-(session) N^*(session)$	262.09	1.28	0.3248	24
$p(session*t) \sigma(session) N^-(session) N^*(session)$	265.73	4.93	0.0527	27
$p(session*t) \sigma(.) N^-(session) \alpha(session*t) N^*(session)$	270.27	9.45	0.0055	28
$p(session*t) \sigma(0) N^-(session) \alpha(session*t) N^*(session)$	271.55	10.74	0.0029	27
2012				
$p(session*t) \sigma(session) N^-(session) N^*(session)$	478.76	0	0.9962	37
$p(session*t) \sigma(0) N^-(session) N^*(session)$	491.40	12.61	0.0018	40
$p(session*t) \sigma(0) N^-(session) \alpha(session*t) N^*(session)$	492.10	13.30	0.0013	41
$p(session*t) \sigma(.) N^-(session) N^*(session)$	494.22	15.43	0.0004	41
$p(session*t) \sigma(.) N^-(session) \alpha(session*t) N^*(session)$	494.90	16.10	0.0003	42
2013				
$p(session*t) \sigma(0) N^-(session) N^*(session)$	360.28	0	0.7175	25
$p(session*t) \sigma(.) N^-(session) N^*(session)$	362.53	2.25	0.2328	26
$p(session*t) \sigma(session) N^-(session) N^*(session)$	367.16	6.88	0.0230	28
$p(session*t) \sigma(0) N^-(session) \alpha(session*t) N^*(session)$	367.42	7.14	0.0202	28
$p(session*t) \sigma(.) N^-(session) \alpha(session*t) N^*(session)$	369.68	9.41	0.0065	29

The overall mean resighting probability was relatively low for all years (average value for years 2011=0.18; 2012=0.15; 2013=0.17), and varied within the same range for the three years (min=0, max=0.37; Figure 2.4). Overall, there were no significant differences between the three years ( $t$ -test  $p>0.16$ ). The 95% confidence intervals varied similarly to the mean resighting probability with few exceptions. For example, year 2012 had the widest (0.15-0.94) and narrowest (0.13-0.14) confidence intervals for a secondary occasion. Estimated confidence intervals were generally wider in

amplitude during 2011 and narrower in 2013, yet I found no significant differences in lower ( $t$ -test  $p>0.18$ ) and upper ( $t$ -test  $p>0.11$ ) limits between years.

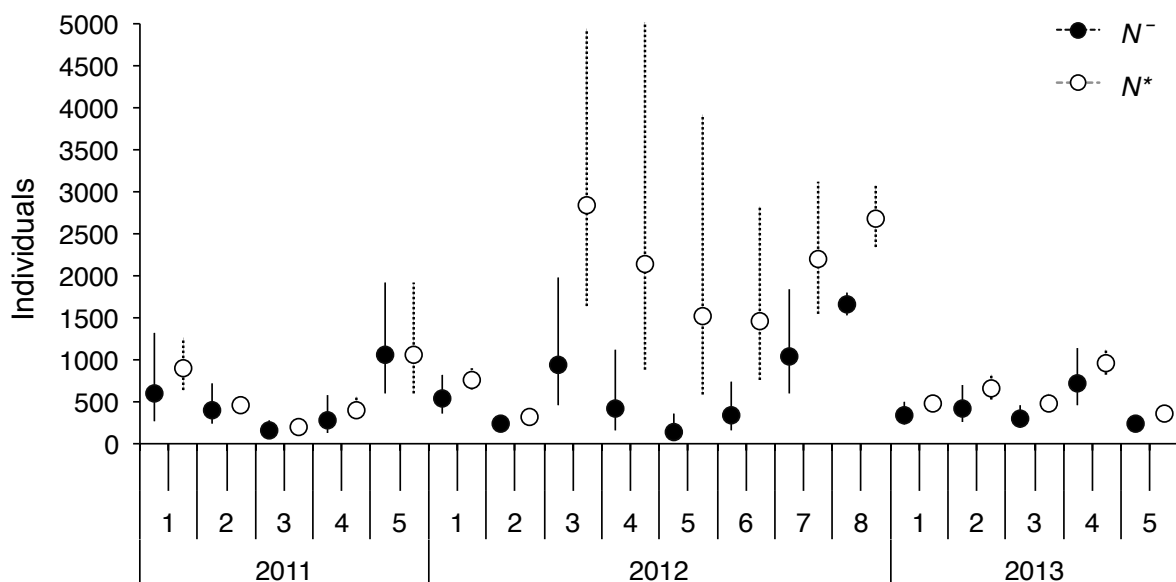


**Figure 2.4** Overall mean resighting probability (*black line*) and 95% confidence intervals (*grey area*) estimated for each secondary occasion (*UVS, M: morning; D: midday; A: afternoon*) from every year.

Estimations of the mean population ( $N^-$ ) and super-population size ( $N^*$ ) from the corrected raw abundances were also variable across primary occasions in all years (Figure 2.5). In 2011, the estimations of super-population size (average 605 ind.; min=203, max=1067) were approximately 1.2 times larger than the mean population size (average 499 ind.; min=158, max=1067). Estimations for year 2012 produced the largest values of super-population size in this study (average 1739 ind.; min=321, max=2842), almost 2.6 times the mean population size (665 ind.; min=144, max=1656). This year was particularly atypical as the lack of marked sharks detected in acoustic receivers, and the reduced raw abundance during the 4th primary interval, affected the estimation of the super population size. In 2013, the estimations of super-population size (588 ind.; min=359, max=958) were on average 1.5 times larger than the mean population size (401 ind.; min=233, max=718). Confidence intervals were the narrowest for both mean population and super-population size in



year 2013, followed by year 2011. Year 2012 experienced an increase in the amplitude of confidence intervals after the third primary occasion, mainly driven by the reduction in the corrected abundance and the absence of marked sharks in the study site. Confidence intervals then tended to shrink as marked sharks returned to the study area. A comparison of the estimations between years showed a significant difference only for the super-population estimations. In 2012, the super-population estimations were significantly larger than those from 2011 ( $t$ -test  $p=0.01$ ) and 2013 ( $t$ -test  $p=0.009$ ).



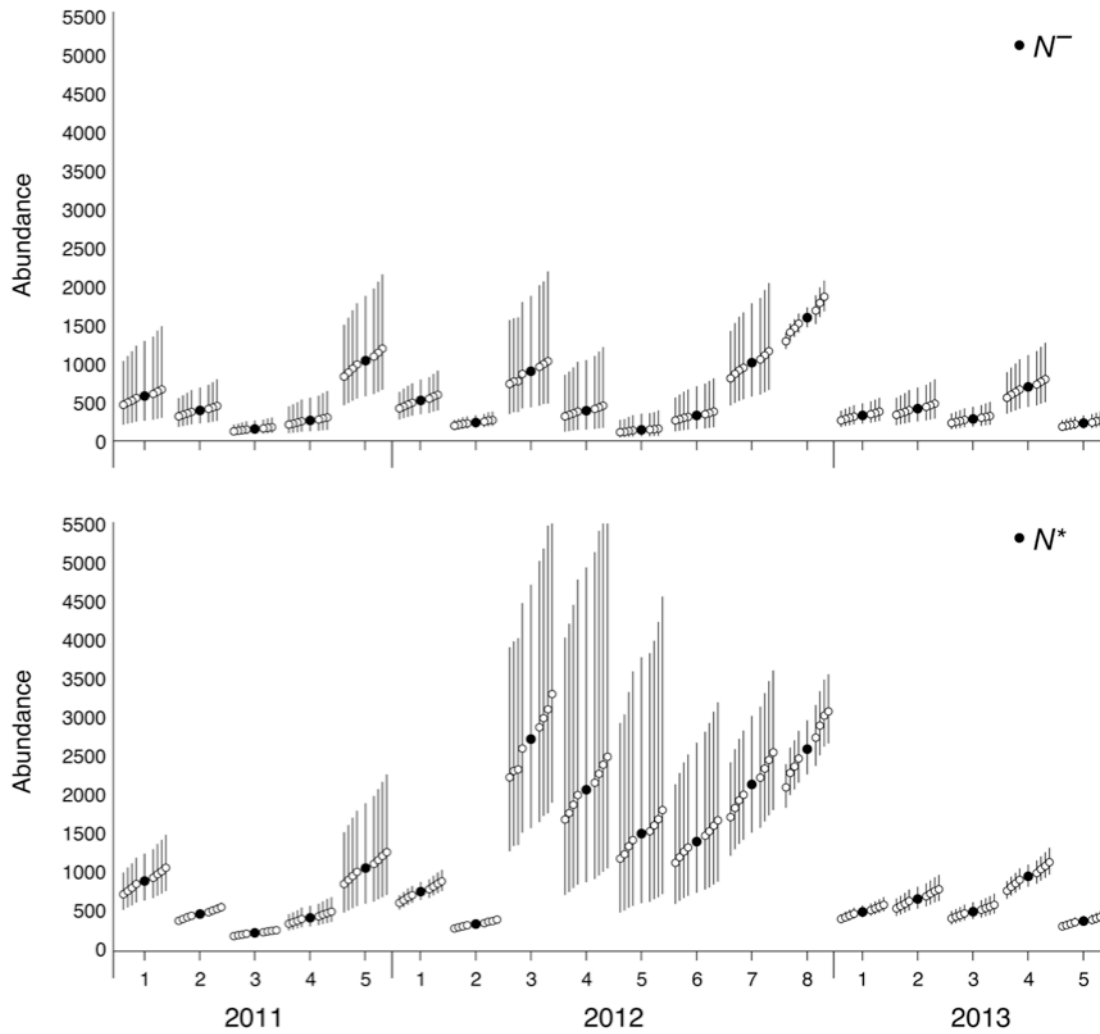
**Figure 2.5** Hammerhead sharks daily (primary occasions) estimations of the mean population ( $N̄$ , black circles) and super-population ( $N^*$ , white circles) size for every fieldtrip.

Simulations showed a varied response of relative bias (PRB), confidence interval length (PCIL) and coverage to changing values of raw abundance. The PRB in the population estimates of every scenario varied at similar magnitude with the under and overestimations of raw abundance (Table 2.4). Contrastingly, PCIL was affected by the level of heterogeneity in sighting probability rather than varying magnitudes in raw abundance. PCIL showed the same trend during each primary sampling

occasion, with increased values in response to increased level of heterogeneity (Figure 2.6). The mean PCIL per year was nevertheless consistent across all scenarios, except when the variation in raw abundance reached  $\pm 20\%$  (Table 2.4). It is noteworthy that mean PCIL values for the mean population estimates were larger than those from super-population estimates, despite the wider confidence intervals observed in year 2012. The coverage shows that if there is a  $\pm 5\%$  variation in the raw abundances, all population estimates across primary occasions still contain the population estimates of the uncorrected raw abundances. This situation becomes less likely when the error is greater than  $\pm 10\%$ , and the level of heterogeneity affects the estimations of population estimates.

**Table 2.4** Percentage of relative bias (PRB), mean percentage of confidence interval length (PCIL), and percentage of coverage for model estimates of mean population size and super-population size in scenarios of under- and overestimation of the raw abundances. Underestimation scenarios are represented by variations of -5% to -20% in raw abundance, and overestimations by variations of 5% to 20%. PRB, PCIL and Coverage are in percentage (%) units.

Raw abundance variation	2011			2012			2013		
	PRB	PCIL	Coverage	PRB	PCIL	Coverage	PRB	PCIL	Coverage
<i>Mean population size</i>									
20%	19.6	140	100	19.8	133	88	19.2	90	100
15%	14.7	140	100	14.5	134	88	14.6	90	100
10%	10.0	140	100	9.8	132	88	9.8	90	100
5%	4.7	140	100	4.7	133	100	4.9	90	100
0%	---	140	---	---	132	---	---	90	---
-5%	-4.7	140	100	-5.0	132	100	-4.7	89	100
-10%	-10.1	140	100	-10.3	131	88	-9.9	89	100
-15%	-14.8	139	100	-14.5	131	88	-14.5	89	100
-20%	-19.7	139	100	-19.5	132	88	-19.3	89	100
<i>Super-population size</i>									
20%	19.6	65	80	19.7	103	63	19.2	38	60
15%	14.8	64	80	14.6	104	75	14.6	38	100
10%	10.0	64	100	9.7	103	100	9.9	38	100
5%	4.7	64	100	4.4	103	100	4.9	38	100
0%	---	64	---	---	103	---	---	38	---
-5%	-4.7	64	100	-5.1	103	100	-4.7	38	100
-10%	-10.1	64	100	-10.3	102	100	-9.9	38	100
-15%	-14.8	64	80	-14.6	102	75	-14.5	38	80
-20%	-19.7	44	40	-19.5	103	63	-19.3	38	40



**Figure 2.6** Hammerhead sharks daily (primary occasions) estimations of the mean population ( $N$ , above) and super-population ( $N^*$ , below) size the under and overestimations of raw abundance. Closed (or filled) circles represent my main model estimation from my uncorrected raw abundance. Open circles represent the underestimated (left) and over estimated (right) raw abundance scenarios. Vertical bars represent the 95% upper and lower confidence intervals.

## 2.5 Discussion

I used the Immigration-Emigration Logit-Normal mark-resight estimator (IELNE; McClintock & White 2012) under an acoustic telemetry-UVS combined approach to estimate the abundance of the endangered scalloped hammerhead shark in the Galapagos. The use of acoustic telemetry to study this species in its habitat is critical

to overcome the constraints of working underwater by allowing to 1) construct reliable encounter histories and estimate the resighting probabilities of marked individuals ([Dudgeon et al. 2015](#); [Pollock et al. 2004](#)); and 2) evaluate the replacement and differential telemetry-UVS sighting probabilities ([Dennhardt et al. 2015](#); [Melnychuk and Walters 2010](#)). My modelling framework provided satisfactory estimations (with narrow confidence intervals) for short-term population size of the hammerhead sharks aggregating at an oceanic hot-spot. These results give support to the use of this method to evaluate the population size of highly mobile pelagic shark species.

### **2.5.1 Population size and structure**

In contrast with visual surveys that count only the visible portion of a population ([Brock 1982](#); [Seber 1982](#)), the mark-resight framework estimates the absolute number of unique (visible and invisible) individuals in a population ([Cooch and White 2014](#)). This is particularly key when assessing status indicators (e.g. survival, density, biomass and reproductive potential) and detecting early changes in wildlife populations ([Cairns et al. 1993](#)).

My estimations of the population size of hammerhead sharks were highly variable yet always fluctuating around a mean of 545 resident individuals (mean population), and a mean of 1100 resident plus transient individuals (super-population). There is only one study that has assessed the population size of hammerhead sharks that could provide a comparable basis to my results. During a single one-day assessment [Klimley and Nelson \(1981\)](#) used free diving to tag and visually count the size of hammerhead schools aggregating at a seamount off the Gulf of California. They reported similar raw abundances (12 to 225 ind.) and size spectra (mean 1.8 m, min

1, max=3.4) of hammerheads, and estimated a population size of 525 individuals. Despite the methodological differences, their findings are similar to my results in terms of raw abundance (0-377 ind.), size structure (160-240 cm) and mean population size (average 2001=499 ind.; 2012=665 ind.; 2013=401 ind.). The similarities in both studies suggest my estimations could provide reliable approximations of the population size of hammerhead sharks in Darwin Island. Furthermore, the relatively low estimates of population size reported by [Klimley and Nelson \(1981\)](#) and my study suggests potential constraints limiting the number of hammerhead sharks aggregating daily in a hot-spot. While this cannot be confirmed, the potential existence of a limited capacity raises important conservation concerns, particularly given this species' observed sexual segregation ([Klimley 1987](#)), and reported global ([Baum et al. 2007](#)) and regional (Chapter 3) decline.

Female-dominated aggregations are regarded to occur as a reproductive strategy of many elasmobranchs to either remain in close proximity to pupping grounds ([Heithaus 2004](#)), or to exploit energy-rich food sources favouring growth and maturation ([Klimley 1987](#)). Although no nursery areas of this species have been reported inside the GMR ([Hearn et al. 2014](#)), there is evidence that suggests these female-biased aggregations could be a common trait in the oceanic hot-spots of the Eastern Tropical Pacific Ocean ([Bessudo et al. 2012](#); [Klimley 1985](#)). My results provide more evidence of this by showing adult and sub-adult female hammerhead sharks dominating the aggregations observed at Darwin's Arch during the three-year study period. Females represent a critical portion of a population that should be protected with greater emphasis to ensure the species' long-term resilience ([Au et al. 2009](#)). If the daily abundance of hammerhead sharks in oceanic hot-spots is constrained by the carrying capacity of the core-refuging habitat, aggregation hot-

spots like Darwin could represent a fragile section of a sub-population of this species foraging in neighbouring off-shore areas. As such, these aggregation hot-spots might be highly susceptible to localized depletion, and could be the underlining reason for the unrecovered, depleted state of hammerheads sharks reported by [Baum et al. \(2007\)](#) at the seamount first studied by [Klimley and Nelson \(1981\)](#).

### **2.5.2 Model assumptions and parameter estimations**

The application of the IELNE has several rigorous assumptions, particularly in regards to sampling without replacement (assumption *iii*) and equivalent sighting probability between the marked and unmarked individuals (assumption *iv*). Despite my efforts to avoid any possible model violation, cryptic body coloration and movement behaviour of fishes can increase the risk of replacement (a violation of assumption *iii*) or differential sighting probability (a violation of assumption *iv*) of individuals while carrying out UVS ([Lincoln Smith 1989](#); [Watson and Quinn 1997](#)). The use of passive and active acoustic telemetry in my analysis show that at least 24% of individuals may have been double-counted (replacement ratio), and that around 26% of the individuals coming into the detection range of the receiver may have had a differential sighting probability from UVS (availability ratio). While violating replacement (assumption *iii*) and availability (assumption *iv*) separately represented significant sources of bias, they almost cancelled each other's effect when correcting raw abundances. Over and undercounting bias cancellation is reported to occur under different methodologies, as noted in the assessment of sharks from fisheries catch data ([Punt et al. 2000](#)), bull trout from redd counts ([Muhlfeld et al. 2006](#)), haddock from experimental fishing ([Collie and Sissenwine 1983](#)), or mountain goats from aerial surveys ([Rice et al. 2009](#)). My simulations of

under- and over counting bias showed that the replacement and availability did not bias final population estimates from corrected raw abundances in comparison to the original uncorrected raw abundances. Corrected raw abundance were 2% larger than the uncorrected raw abundances, yet simulations showed only deviations greater than 5% could considerably bias populations estimates. This result supports the use of my combined telemetry-UVS mark-resight approach by showing that the behaviour of the species did not affect the replacement and availability of the species to be counted during sampling periods. It is reasonable to assume that under- and over-counting bias cancellation does not imply a norm, as both replacement and availability can vary considerably depending on the species under assessment ([e.g. Dennhardt et al. 2015](#)). To avoid potential violation of these model assumptions, both replacement and availability should be carefully evaluated in regards to the species behaviour and sampling area.

The selection of individuals to be marked (by acoustic telemetry) can also produce differences in the sighting probability (assumption *iv*) if they are not a representative subset of the population to be resighted (by UVS) ([McClintock and White 2012](#)). Sharks were tagged whenever schools passed near by or directly over the reef area. The only restrictive criterion to tag sharks was depth, as free-divers diving capacity was restricted to depths shallower than 15meters. While all sharks tended to evade divers, successful tagging only occurred when divers took advantage of the individuals' blind spot, by diving from straight above a shark, regardless of the animal's depth.

[Klimley \(1983\)](#) and [Ketchum et al. \(2014a\)](#) have reported that hammerhead sharks swimming in aggregation areas constantly vary their depth from the bottom to the surface. This random depth variation in sharks suggests any shark in the study site

could have been at a free-diver's reach. The lack of significant differences between the total length of the marked and observed sharks further supports considering the marked individuals as representative of the sampled population.

My results showed that population size estimates were particularly sensitive to the level of heterogeneity in resighting probability of my data. [Neal et al. \(1993\)](#) reported that the levels of heterogeneity can be particularly affected by the behaviour of the species and the environmental conditions. A marked reduction in the raw abundance, lack of acoustic detections and sustained reduction of current strength at the Darwin's Arch provided evidence of this during the third to fifth primary intervals of 2012. Despite AIC values supporting models full time- and session-dependant in the resighting probability, the temporary emigration of marked and unmarked sharks in the middle of 2012 was unfortunate for estimation purposes. Hammerhead sharks are known to constantly arrive and/or depart from oceanic islands and seamounts across the Eastern Tropical Pacific ocean ([Bessudo et al. 2011](#); [Klimley et al. 1993](#)), including Darwin Island ([Ketchum et al. 2014b](#)). The resulting rapid turnover of individuals in response to the oceanographic conditions could imply that the studied population was mostly comprised of transient rather than resident individuals. A similar scenario of low resighting probability and rapid turnover (less than two days) was reported for photo-identified whale sharks also aggregating at Darwin's Arch ([Acuna-Marrero et al. 2014](#)). This scenario becomes increasingly likely when assessing a highly mobile species in a highly dynamic environment, and should be carefully considered in the design of future studies. I recommend that additional research should be carried out to review the inclusion of environmental variables (e.g. water visibility, current strength, thermocline depth, water temperature, etc.) within the modelling framework to improve parameter estimations. The use of a



larger number of tags would increase the probability of tagging more resident sharks and reduce the effect of the level of heterogeneity in population estimates. This is seen in my study where both years 2011 (ten tags) and 2013 (twenty tags) produced fairly stable estimations of mean population and super-population size, however the latter year produced the narrowest confidence intervals.

These results provide support to use this approach as an alternative tool for monitoring the population size of this endangered species in aggregation hotspots, and suggest a highly variable yet relatively low daily abundance (~545ind.) of residents, and low daily confluence (~1100ind.) of resident and transient hammerhead sharks. They also provide a solid baseline for transitioning the use of this approach to other marine species; however, specific behavioural and environmental traits should be carefully reviewed to reduce the likelihood of model violations. The use of telemetry is not only a helpful tool for resighting individuals in the field but also for aiding the evaluation of model violation and adjusting raw counts. This approach provides a less invasive alternative that could reduce the stress factor on hammerheads posed by the elevated post-capture mortality associated with fishing methods ([Gulak et al. 2015](#)). Furthermore, a simultaneous assessment of Darwin Island with nearby 'aggregation' islands is also recommended to 1) explore the existence of potential constraints limiting the resident population size of hammerhead sharks at aggregation hot-spots; and 2) explore the feasibility of scaling up estimations of the super-population (residents and transients individuals) size to the entire northern GMR.

## **Chapter 3** *Evaluating abundance trends of iconic species using local ecological knowledge*

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### **3.1 Abstract**

Wildlife abundance is commonly used to assess the status of wildlife populations and their responses to changes in management frameworks. Unfortunately, monitoring abundance trends often requires long-term data collection programs, which are not always carried out due to adverse environmental conditions, lack of economic resources and or insufficient planning. One alternative to scientific surveys is to utilise local ecological knowledge (LEK), which has proven accurate when assessing the population status of many wildlife species and in determining the effectiveness of different management regulations, such as the creation of protected areas. Here I developed a LEK-based approach to assess historical wildlife population trends by using the ecological knowledge of non-extractive resource users. Specifically, I assessed the recollections of dive guides regarding the abundance trends of six shark species in the Galapagos Marine Reserve (GMR). I explored dive guides' experience and knowledge on shark population status and issues within the reserve, and their perceived trends since the 1980s. Based on dive guides' trend perceptions, I developed a virtual abundance change (VAC) model to assess the deficit or surplus in abundance for the decades following the 1980s. In general, dive guides showed consensus for negative trends for all shark species, and suggested fisheries as the major factor driving abundance trends of sharks in Galapagos. VAC model results suggest that hammerhead and whitetip reef sharks have experienced the most consistent perceived decline over the last four decades. Silky sharks and Galapagos sharks also experienced perceived declines but later stabilized. Whale shark

abundance was perceived as stable across the study time frame, while blacktip sharks were the only species perceived to have increased in abundance in recent decades. Comparing the VAC results with empirical datasets from the GMR and the Eastern Tropical Pacific provided corroborating evidence that the dive guides' ecological knowledge has described the abundance fluctuations of all except silky sharks. This study is an important addition to the growing literature regarding the value of LEK in assessing the state of marine resources in data-limited management regions. My VAC method offers an alternative approach by which LEK can provide valuable insights into the historical trends in iconic species abundance.

### **3.2 Introduction**

The primary objective of population assessment is to collect data on population size and structure to identify trends (i.e. increasing, stable, decreasing) in plant or animal populations ([Meffe and Carroll 1997](#)). Abundance is a predictor commonly used to assess the long-term persistence and extinction risk of a population ([Sutherland 1996](#)), and to assess the species response to adopted management frameworks, such as harvesting regulations or the creation of protected areas (e.g. [Gillingham et al. 2015](#); [Lubchenco et al. 2007](#)). Unfortunately, monitoring abundance trends often requires long-term data collection programs, which are not always carried out due to adverse environmental conditions, lack of economic resources or insufficient planning ([Chambers et al. 2014](#); [Claudet and Guidetti 2010](#); [Johannes 1998](#)). This lack of scientific data hampers the evaluation of wildlife, and consequently, the adoption of different management alternatives to deal with conservation issues ([Ludwig et al. 1993](#); [Walters 1986](#)).

An alternative to this issue is to explore the local ecological knowledge (LEK) of people who have continuous interactions with the environment/resources ([Davis and Wagner 2003](#)). LEK is associated with people whose livelihood largely depends on a natural resource, either through extractive or conservation activities ([Brook and McLachlan 2008](#)). LEK is often criticized because perceptions are affected by cultural beliefs and the economic importance of the exploited resource ([Gilchrist et al. 2005](#); [Howard and Widdowson 1996](#)). However, it has now been widely used in a diverse number of cases and shown to be indicative of the population status and trends of birds (e.g. [Gilchrist et al. 2005](#); [Gregory et al. 2004](#)), lobsters (e.g. [Eddy et al. 2010](#)), and sharks and fishes (e.g. [Taylor et al. 2011](#)), trends in ecological processes (e.g. [Poizat and Baran 1997](#); [Rochet et al. 2008](#)) and fisheries dynamics (e.g. [Ainsworth et al. 2008](#); [Neis et al. 1999](#)). As such, LEK is becoming an important tool in assisting the evaluation of different resource management frameworks, such as fisheries community-based management ([Hoggarth et al. 2006](#)) or the establishment of marine protected areas ([MPA](#); e.g. [Friedlander et al. 2003](#)) and their potential to preserve or rebuild fish stocks (e.g. [Gerhardinger et al. 2009](#); [Yasué et al. 2010](#)).

Resource development and management schemes have often been designed without significant historical information on the state of their resources ([Wolff 2009](#)). This is especially true in marine management where the widespread lack of biodiversity baselines hampers the evaluation of the conservation state of resources and the effectiveness of adopted management frameworks. The Galapagos Marine Reserve (GMR) is a case in point. Few ongoing projects are dedicated towards monitoring the abundance and distribution of biodiversity over a sufficient time scale to test the effect of reserve creation ([Danulat and Edgar 2002](#)). Yet there are still important gaps of information regarding many charismatic megafauna, such as sharks ([Hearn et al.](#)

[2014](#)). The life history traits of sharks makes them one of the most vulnerable taxa to overfishing ([Compagno et al. 2005](#)), with many shark species now classified as being at risk of extinction ([Dulvy et al. 2014](#)). In the GMR, the management framework adopted in 1989 has protected sharks from fishing and trading ([WildAid 2010](#)), in response to the fishing pressure they face inside the reserve ([Carr et al. 2013](#); [Reyes and Murillo 2007](#)) as well as around the Eastern Tropical Pacific Ocean ([ETP](#); [Watts and Wu 2005](#)). It is suggested that the size of the reserve, coupled with the effect of El Niño Southern Oscillations and the adopted management framework, may have favoured the recovery of some shark populations (Wolff et al. 2012). However, the lack of long-term monitoring in the Galapagos hinders the evaluation of the population trends of shark species and confirmation of any rebuilding trend.

Here I developed an alternative approach to scientific surveys to assess wildlife historical population trends – instead using the ecological knowledge of non-extractive resource users. Particularly, I was interested in capturing users' knowledge to assess how shark populations have changed through time to the present abundance levels. To achieve this, I developed a semi-quantitative analysis method that evaluates population trends rather than quantifying numerical abundances. I tested my approach using the recollections of dive guides (hereafter “divers”) regarding abundance of six shark species found in the GMR. I constrained my assessment to the decades since the 1980s to coincide with the expansion of the dive tourism industry in Galapagos ([Danulat et al. 2003](#)). Given the divers' reliable presence in the main dive sites across the GMR, they are considered important LEK holders. I tested their knowledge against published and unpublished data on shark trends from fish surveys carried out in Galapagos and across the ETP.

### 3.3 Methods

#### 3.3.1 Study site

The GMR is currently the largest MPA in the Eastern Pacific Ocean and hosts the most functionally diverse fish communities worldwide ([Stuart-Smith et al. 2013](#)). This extraordinary suite of species has attracted fishermen and conservationists from across the globe, and consequently, produced several disputes over resource use and sustainability ([Camhi 1995](#); [Merlen 1995](#)). Large predatory fish, such as sharks, have experienced increased fishing pressure since the early 1950s from international fishing fleets targeting sharks for their fins ([Carr et al. 2013](#); [INP 1964](#); [Reyes and Murillo 2007](#)). The Ecuadorean Government imposed a ban on shark fishing and trading in 1989 ([SRP 1989](#)), in response to the recognition of the sharks' vulnerability to fisheries and pressure from local fishermen and tourism sectors who denounced industrial fishing of sharks ([Fenopader 1989](#)). This protective scheme has since been improved by regulating the use of fishing gear with high levels of by-catch ([GNPS 1998](#); [Murillo et al. 2004](#)), installing high-technology patrolling and surveillance to seize poachers ([DPNG 2009](#)) and enforcing legal processes ([WildAid 2010](#)). Unfortunately, illegal fishing still occurs in the GMR, however, the magnitude and dynamics are unknown ([Carr et al. 2013](#)). In contrast to fishing, the dive tourism industry started in Galapagos in the mid-1980s, and since then sharks have been a main attraction (Hearn et al. 2014). Over the last decades the dive industry has grown considerably even though growth has been at a slower rate than land-based tourism ([Cubero 2008](#)). Divers have been visiting the same sites around the archipelago, although the most common are close to the islands of Darwin and Wolf ([Danulat et al. 2003](#)). Although authorities track site use and frequency of visits by tour operators,

there are no official records of the total number of divers who have worked in this industry since it started.

### **3.3.2 Data collection**

The Directorate of the Galapagos National Park held a series of compulsory seminars (July-November of 2013) directed at guides currently working in the Galapagos Islands to deliver the most up-to-date information on scientific research and conservation efforts in the area. It is noteworthy that none of the presentations during the seminars covered the population status and trends of sharks in the GMR, as this information was unknown. During this time, questionnaires were provided to divers who were known to have been guiding in the GMR for more than five years. Given the lack of records of all divers who have worked for the tourism industry, I implemented a section at the end of the questionnaire asking divers to name others known to have experience guiding in the GMR. I limited my survey to divers who had more than five years guiding to ensure their experience was sufficient to detect possible changes in the abundance of the target species. A total of 35 divers were approached and handed the questionnaires, however, only 25 returned completed surveys.

My questionnaires focused on assessing the status of the six most common shark species found across dive sites in the GMR ([Danulat et al. 2003](#); [Zarate 2002](#)). This selection comprised blacktip sharks (*Carcharhinus limbatus*), Galapagos sharks (*C. galapagensis*), hammerhead sharks (*Sphyrna lewini*), silky sharks (*C. falciformis*), whale sharks (*Rhincodon typus*) and whitetip reef sharks (*Triaenodon obesus*). These species represent a range of biological, ecological, and fishery susceptibility combinations (Table 3.1). They are found from coastal to pelagic ecosystems

displaying either restricted or broad-scale movements, which influences their susceptibility to fisheries operating inside and around the GMR.

Questionnaires were carefully designed to express neutral, unpolarised questions that avoided influencing divers with predetermined answers (Figure 3.1). Questionnaires were designed to collect information on *i)* the years and places of divers' experience, *ii)* their overall perception of change (if any), *iii)* factors causing the perceived changes, *iv)* decadal perception of change per species using predetermined trend scores, and *v)* a quantification of the trend scores. In the first section, divers were requested to state the years and the bioregions ([as in Edgar et al. 2004](#)) they visited while actively working for the tourism industry. The second and third sections were intended to understand if they held any general perceptions regarding shark abundance trends across the whole GMR, and the reasons for these perceptions, if any. These questions were used to crosscheck the following sections of the questionnaire. The fourth section asked the divers to state their perception of abundance change for the six species across the whole GMR, within the 1980s, 1990s, 2000s and 2010s. The current decade (2010-2019), although incomplete, was incorporated into the analysis to provide an additional reference point to compare with ongoing empirical data collection projects. I provided divers with five predefined categorical scores: major decline (MD), decline (D), stable (S), increase (I), and major increase (MI). Finally, I requested divers to state how much each categorical score meant to them in terms of their perceived abundance change. I requested them to state these values in percentages (e.g. "decline" may equate to 25% in abundance reduction; "major increase" to a 70% increase in abundance). The information from this last section was used as an indication of the relative abundance each decade as perceived by each dive guide.





Parque Nacional  
**GALÁPAGOS**  
Ecuador



ÁREAS  
PROTEGIDAS  
POR TI.



Ministerio  
del Ambiente

The main objective of this questionnaire is to assess the perception of the dive guides working in the Galapagos Marine Reserve in regards to the abundance of six shark species. The Directorate of the Galapagos National Park thanks your collaboration with any information you could provide in this questionnaire. This information will be analysed to understand any changes these sharks' species could have incurred. No personal information collected will be disclosed at any time.

#### A) EXPERIENCE

1) Age: \_\_\_\_\_ Nationality: \_\_\_\_\_

2) Which activity do you currently do? \_\_\_\_\_

3) How many years of experience do you have (per activity)?

Activity	Years	Activity	Years
Photography		Science	
Dive guide		Other:	

4) Could you state in which regions, and how many years of experience do you have per region?

Region	Years
North (Darwin, Wolf, Roca Redonda, Marchena, Pinta and Genovesa)	
South (Floreana, Española, neighbouring seamounts and islets)	
West (Fernandina and western Isabela)	
Centre (Santa Cruz, Santiago, San Cristobal, and northeast and southeast Isabela)	

#### B) ABUNDANCE

1) Have you notice any change in the abundance of sharks in your years of experience? No \_\_\_\_ Yes \_\_\_\_

If **NO**, jump to **section C**.

2) If you noticed changes in the abundance of sharks, how would you rate this change? Positive \_\_\_\_ Negative \_\_\_\_

3) Would you be able to state per species and per decade if you observe any change in the abundance of the following shark species? Please use the following scale:

**Major increment (MI), Increment (I), Stable (S), Decrease (D), Major decrease (MD)**

Decade	Hammerhead s.	Blacktip s.	Whale shark	Galápagos s.	Silky s.	Whitetip reef s.
1980						
1990						
2000						
2010						

4) Could you state which is for you the meaning of the used trend scales in terms of percentage of change?

Major decrease (MD) \_\_\_\_\_% Decrease (D) \_\_\_\_\_%

Increment (I) \_\_\_\_\_% Major increment (MI) \_\_\_\_\_%

5) Could you name which factors you believe are affecting the abundance of the previously named sharks?

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#### C) ADDITIONAL INFORMATION

1) Would you like to be contacted in the future?

Name: \_\_\_\_\_ E-mail: \_\_\_\_\_

2) Could you name other diver that have worked for more than five years guiding in the Galapagos Marine Reserve

Name	Current occupation	Contact

3) DO YOU HAVE ANY COMMENT OR ADDITIONAL INFORMATION YOU WOULD LIKE TO SHARE?

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**Figure 3.1** Questionnaire used by the Directorate of the Galapagos National Park to assess the perception of divers in relation to potential abundance changes in six shark species. This questionnaire was originally designed and delivered to dive guides in Spanish. This figure represents the closest possible translation into English to show the neutrality of the questions asked to divers.

**Table 3.1** Description of relevant ecological, conservation and fisheries features for the six shark species under assessment.

Species	2010-2013 average abundance <sup>1</sup> (Ind./hour*dive)	Habitat type <sup>2</sup>	Residence in GMR (%) <sup>3</sup>	Nursery grounds <sup>4</sup>	Conservation status <sup>5</sup>	Misidentification risk <sup>6</sup>	Susceptibility to coastal fisheries inside GMR <sup>7</sup>	Susceptibility to pelagic fisheries inside GMR <sup>8</sup>	Fishing susceptibility outside Reserve <sup>9</sup>
Blacktip shark	4	Reef associated	High	Yes	Near threatened	Low	Medium	Medium	Low
Galapagos shark	8	Reef associated	High	Yes	Near threatened	High (with silky sharks)	Medium	Medium	Low
Scalloped hammerhead shark	51	Semi-pelagic, oceanodromous	Medium	Probable	Endangered	None	Low	High	High
Silky shark	2	Semi-pelagic, oceanodromous	Medium	Probable	Near threatened	High (with Galapagos sharks)	Medium	High	High
Whale shark	2	Pelagic, oceanodromous	Low (Seasonal)	No	Vulnerable	None	None	None	Low
Whitetip reef shark	2	Reef associated	Permanent	Yes	Near threatened	None	Low	None	None

<sup>1</sup>: Data for all the GMR collected by the Pelagic Fish Survey program (Hearn A/CDF-UCD-DPNG, *unpublished data*). <sup>2</sup>: [Compagno et al. \(2005\)](#). <sup>3</sup>: [Acuna-Marrero et al. \(2014\)](#); [Hearn et al. \(2013\)](#); [Hearn et al. \(2014\)](#); [Peñaherrera C, \(unpublished\)](#). <sup>4</sup>: [Hearn et al. \(2014\)](#); [Llerena et al. \(2015\)](#). <sup>5</sup>: [Baum et al. \(2007\)](#); [Bennett et al. \(2003\)](#); [Bonfil et al. \(2009\)](#); [Burgess and Branstetter \(2009\)](#); [Norman \(2005\)](#); [Smale \(2005\)](#). <sup>6</sup>: [Compagno et al. \(2005\)](#) and Shillinger G, (*pers.com*). <sup>7</sup>: Based on the risk assessment published by [Peñaherrera and Hearn \(2008\)](#). <sup>8</sup>: Based on the sharks occurrence in experimental longline fishing projects, reported seizures of illegal shark catches and risk assessments by [Carr et al. \(2013\)](#); [Hearn et al. \(2014\)](#); [IATTC \(2010\)](#); [Murillo et al. \(2004\)](#); [Reyes and Murillo \(2007\)](#). <sup>9</sup>: Based on catch statistics and risk assessments in Ecuadorean and ETP waters by [IATTC \(2010\)](#); [Martinez-Ortiz et al. \(2015\)](#).

### 3.3.3 Data analysis

I binned positive (I and MI) and negative scores (D and MD), as well as the guides' years of diving experience (Low: 5 to 10 years; Medium: 10 to 20; and, High: 20 or more) to simplify the data description and allow the following statistical analysis. I used the  $\chi^2$  goodness-of-fit tests ([Lancaster 2004](#)) to search differences in the categorical trend scores per decade, and logistic regression models ([Jaeger 2008](#)) to explore the effect of the level of experience and decades on the frequency of the obtained scores. Furthermore, I tested differences in the percentage of abundance change scores per level of experience by running One-way Analysis of Variance ([Zar 2010](#)).

A semi-quantitative virtual abundance change (VAC) model was then created in order to estimate the species virtual abundance across decades. The model uses an initial virtual abundance value of 1, and then calculates the remnant or surplus in abundance for the following decades by transforming the categorical trend scores and the percentage of abundance change into virtual abundances. The model is based on the following equation:

$$V_{ka} = X_{k-1} \pm (X_{k-1} * Y_{Zka}) \quad (1)$$

where  $V$  is the virtual abundance value estimated for decade  $k$  and dive guide  $a$ .  $X$  is an average of all the virtual abundance size values for all guides of the decade  $k-1$ .  $Y$  is the percentage of perceived abundance change of the corresponding categorical score  $Z$  for decade  $k$  and diver  $a$ . It is important to note that when  $k$  was equal to 1980s,  $X_{k-1}$  was set as the initial virtual abundance value. Moreover, when  $k$  was not equal to 1980s,  $X_{k-1}$  represented the average of the virtual abundance values of all divers from the previous decade to reduce the effect of shifting baselines ([Ainsworth et al. 2008](#)).

Divers who started diving in decade  $k$  did not observe the same abundance as divers who dived in decade  $k-1$ , but the remnant or surplus of abundance from  $k-1$ . With these considerations, a logic rule was then created to estimate the virtual abundance per decade per diver based on the categorical trend scores as follows:

$$\text{if } Z_k = S, \quad \text{then } V_{ka} = X_{k-1} \quad (2)$$

otherwise

$$\text{if } Z_k = MD, \quad \text{then } V_{ka} = X_{k-1} - (X_{k-1} * Y_{DM\ ka}) \quad (3)$$

otherwise

$$\text{if } Z_k = D, \quad \text{then } V_{ka} = X_{k-1} - (X_{k-1} * Y_{D\ ka}) \quad (4)$$

otherwise

$$\text{if } Z_k = I, \quad \text{then } V_{ka} = X_{k-1} + (X_{k-1} * Y_{I\ ka}) \quad (5)$$

otherwise

$$\text{if } Z_k = MI, \quad \text{then } V_{ka} = X_{k-1} + (X_{k-1} * Y_{MI\ ka}) \quad (6)$$

Final results were plotted as the average virtual abundance per decade with its corresponding upper and lower standard deviation. I used the standard deviation as a measure of the model variance and level of agreement. A third-order polynomial trend line was fitted to observe smoothed changes in virtual abundance per decade.

I validated the model efficiency by comparing my VAC model results for hammerhead, Galapagos and whitetip reef sharks with available abundance information from Pelagic Fish surveys (Hearn A/CDF-UCD-DPNG, *unpublished data*) and Reef Fish surveys (Banks S/Charles Darwin Foundation, *unpublished data*) carried out within the GMR. In addition, I used published information from Cocos Island ([White et al. 2015](#)), which is 700 km from the GMR, and Malpelo Island ([Soler et al. 2013](#)), which is 1200 km from the GMR. Both MPAs are the closest to the GMR and held the most similar shark and fish assemblages. I standardized the abundance data from Cocos,

Malpelo and GMR Pelagic surveys as the natural logarithm of the counted sharks per dive plus one, following [Friedlander et al. \(2012\)](#). Data from the Galapagos Reef fish surveys is presented as the number of individuals per square meter ([Edgar et al. 2004](#)). The two datasets from Galapagos (reef fish and pelagic surveys) represent the averaged relative abundance for all the monitored sites across the GMR, in order to be consistent with the spatial scale used in the questionnaires.

### **3.4 Results**

Twenty-five of 35 identified guides completed and returned questionnaires suitable for inclusion. The other divers preferred not to participate in this survey, did not properly fill out the questionnaires or had less than the minimum required experience. The average age of divers was 43 years old (Table 3.2). The maximum time divers had been operating was 30 years, and the minimum was five years (as the chosen cut off). The number of divers who have actively worked increased from 4 in the 1980s to 25 in the last two decades with the addition of more divers with correspondingly less experience. The spatial distribution of diver experience in three experience groups was relatively homogeneous for the north, south and central bioregions. In the less experienced group (5-10 years), only one diver did not have any experience in the north, one lacked experience in the central area, and four lacked experience in the west. The medium experience group (10-20 years) had the most homogeneous distribution across bioregions, with only one diver lacking experience in the north, and two in the west. For the most experienced group (20-30 years), one diver lacked experience in the south, one in the central, and three in the west region.

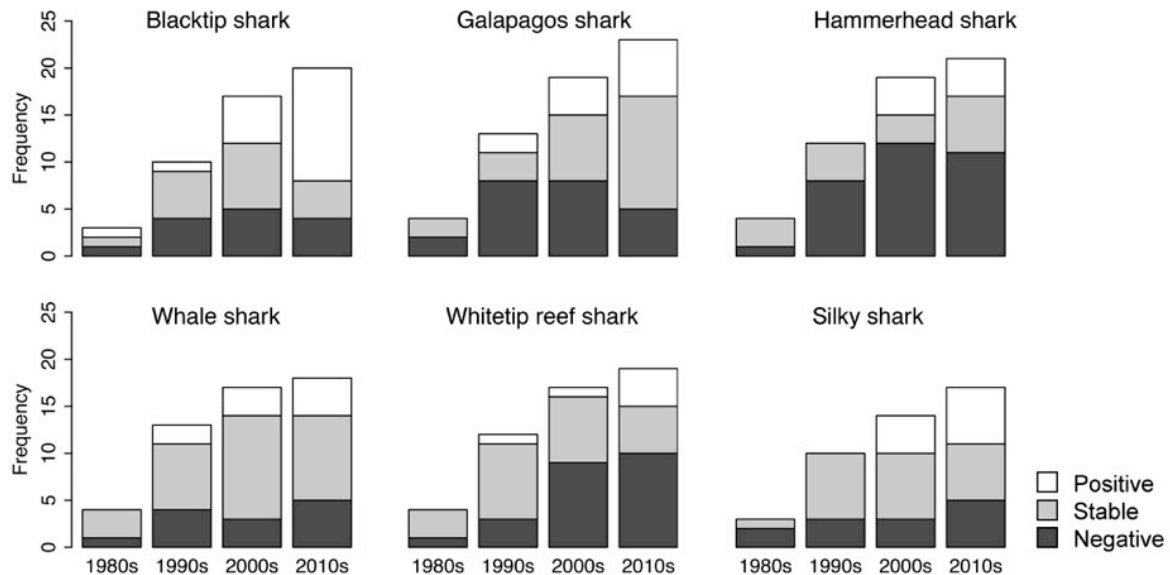
**Table 3.2** Number of divers per decade and bioregion grouped according to their dive experience.

Years of experience	N	Age of divers			Active divers per decade				Active divers per bioregion			
		Aver.	Max	Min	1980s	1990s	2000s	2010s	North	South	West	Central
5-10	7	41	56	31	--	--	7	7	6	7	3	6
10-20	11	44	60	36	--	7	11	11	10	11	9	11
20-30	7	45	50	38	4	7	7	7	7	6	4	6
<b>Total</b>	<b>25</b>	<b>44</b>	<b>30</b>	<b>5</b>	<b>4</b>	<b>14</b>	<b>25</b>	<b>25</b>	<b>23</b>	<b>24</b>	<b>16</b>	<b>23</b>

The majority of interviewed divers (82%) perceived changes in the abundance of shark species during their career. Overall, 67% observed changes they perceived as “negative” in all species, 24% perceived changes as “positive” across all species, and the remaining 9% perceived changes that varied between species. Factors that negatively affected shark trends were primarily perceived as driven by local and external fishing operations (70% of answers). Other factors that were perceived to affect shark population were tourism-related activities (8%), such as navigation and excessive use of diving sites, as well as changes in the oceanographic conditions (7%) due to climate change and ENSO events.

Despite the majority of divers indicating that they observed negative changes, detailed analysis showed that perception varied according to the species and decade (Figure 3.2). The  $X^2$  goodness of fit test showed that for all species, except whale sharks, there are significant differences in the observed frequency of categorical scores per decade ( $p < 0.03$  for those five species; Table 3.3). For blacktip sharks, the most common perception score was “stable” during the 1990s and 2000s, with increasing positive scores (I and MI) towards the 2010s. For the Galapagos shark, negative trend scores (MD and D) were the most common answers from 1980s to 2000s, with stable trend scores becoming the most frequent answer for 2010s. Hammerhead shark had the highest number of negative trend scores across all decades, although positive and stable scores increased for the last two recorded

decades. Scores for silky sharks were predominantly negative in the 1980s, while stable scores were more common in the 1990s and 2000s. Whitetip reef sharks were mostly scored as stable in the first two decades, with trends becoming increasingly negative.



**Figure 3.2** Obtained trend scores summarizing shark populations based on divers' perception of abundance change. *Positive* category includes the obtained frequency of increase and major increase scores; and, *Negative*, decrease and major decrease scores.

While there was variability in the categorical trend scores, I found no effect of diver's level of experience on the trend scores or in the perceived percentage of abundance change. Logistic regression models did not show evidence for complete dependence on the level of experience with the decade and trend scores across sharks ( $p=0.29$  for three-way interaction; Table 3.3). Also, there was no evidence of association in the minimal adequate models for this data set in the interactions between the level of experience and decades ( $p=0.8$  for two-way interaction) and the level of experience and trend ( $p=0.27$  for two-way interaction). The one-way ANOVA showed no

significant differences (for all categories ANOVA  $p=0.38$ ,  $df=2$ ) in the perceived percentage of abundance change across the levels of experience (Table 3.4).

**Table 3.3**  $X^2$  goodness of fit and log-linear model deviance test results for the categorical data obtained from the divers interviews. *LoE*: level of experience.

Species	Chi-Squared		Log-linear models					
	Decade x Trend		Three-way interactions		Two-way interactions			
			LoE x Decade x Trend		LoE x Decade		LoE x Trend	
	$X^2$	$p$	LRT	$p (X^2)$	LRT	$p (X^2)$	LRT	$p (X^2)$
<i>Blacktip shark</i>	8.14	0.02	0.73	0.865	0.80	0.939	0.71	0.950
<i>Galapagos shark</i>	6.86	0.03	1.88	0.598	0.80	0.977	3.88	0.423
<i>Hammerhead shark</i>	8.54	0.01	4.65	0.969	1.79	0.938	5.17	0.271
<i>Silky shark</i>	7.79	0.02	3.75	0.290	2.23	0.816	1.74	0.629
<i>Whale shark</i>	2.14	0.34	1.48	0.831	1.52	0.911	1.54	0.672
<i>Whitetip reef shark</i>	8.10	0.02	3.40	0.494	2.31	0.805	2.74	0.602

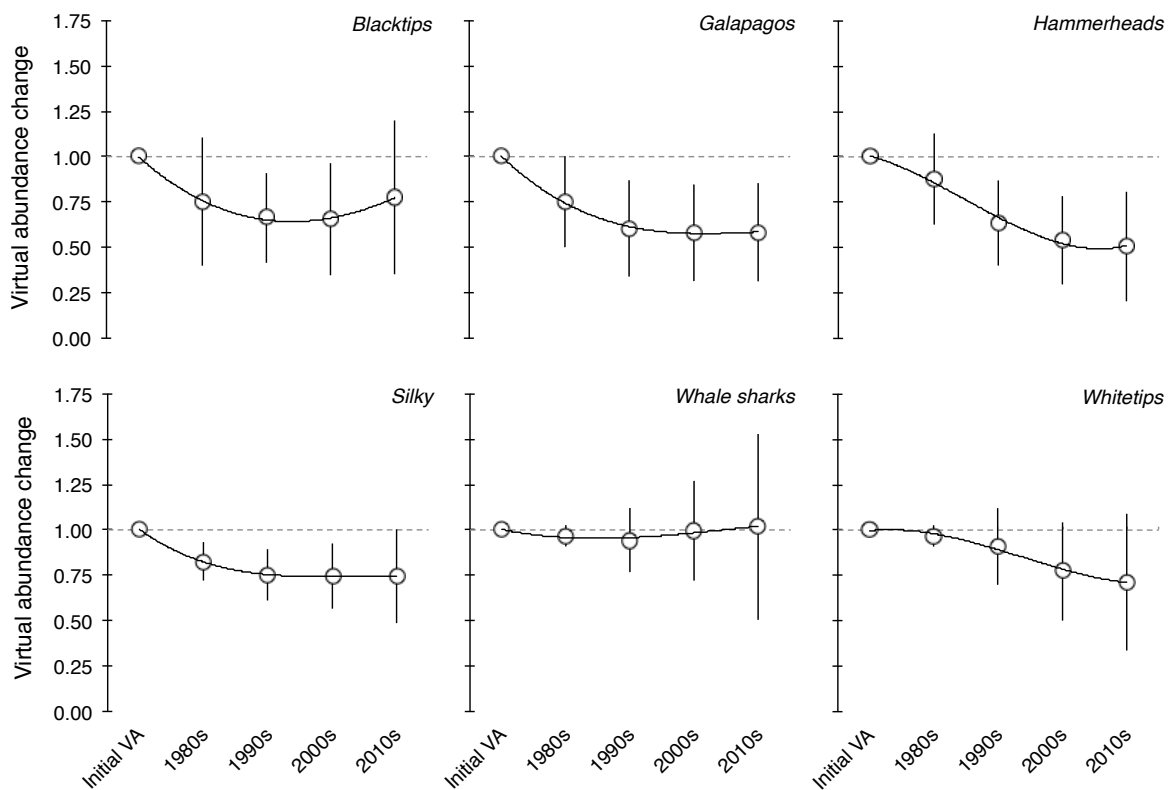
**Table 3.4** Differences in the perceived percentage of abundance change values per categorical score (stable was not included in this analysis), level of diver experience, and the one-way ANOVA test results for comparing differences between the levels of diver experience per categorical score.

	MD	D	I	MI
<i>Overall results</i>				
Min	0.20	0.10	0.20	0.30
Max	0.70	0.50	0.50	0.70
Mean	0.53	0.27	0.29	0.51
Mode	0.50	0.30	0.30	0.50
<i>Level of Experience</i>				
<i>Low (5-10yrs)</i>				
Mean	0.60	0.29	0.29	0.60
s.d.	0.14	0.10	0.10	0.14
<i>Medium (10-20 yrs)</i>				
Mean	0.48	0.25	0.27	0.40
s.d.	0.19	0.09	0.04	0.14
<i>High (20-30 yrs)</i>				
Mean	0.53	0.30	0.30	0.52
s.d.	0.10	0.10	0.10	0.11
<i>One way ANOVA</i>				
<i>df.</i>	2	2	2	2
<i>p</i>	0.716	0.456	0.822	0.381

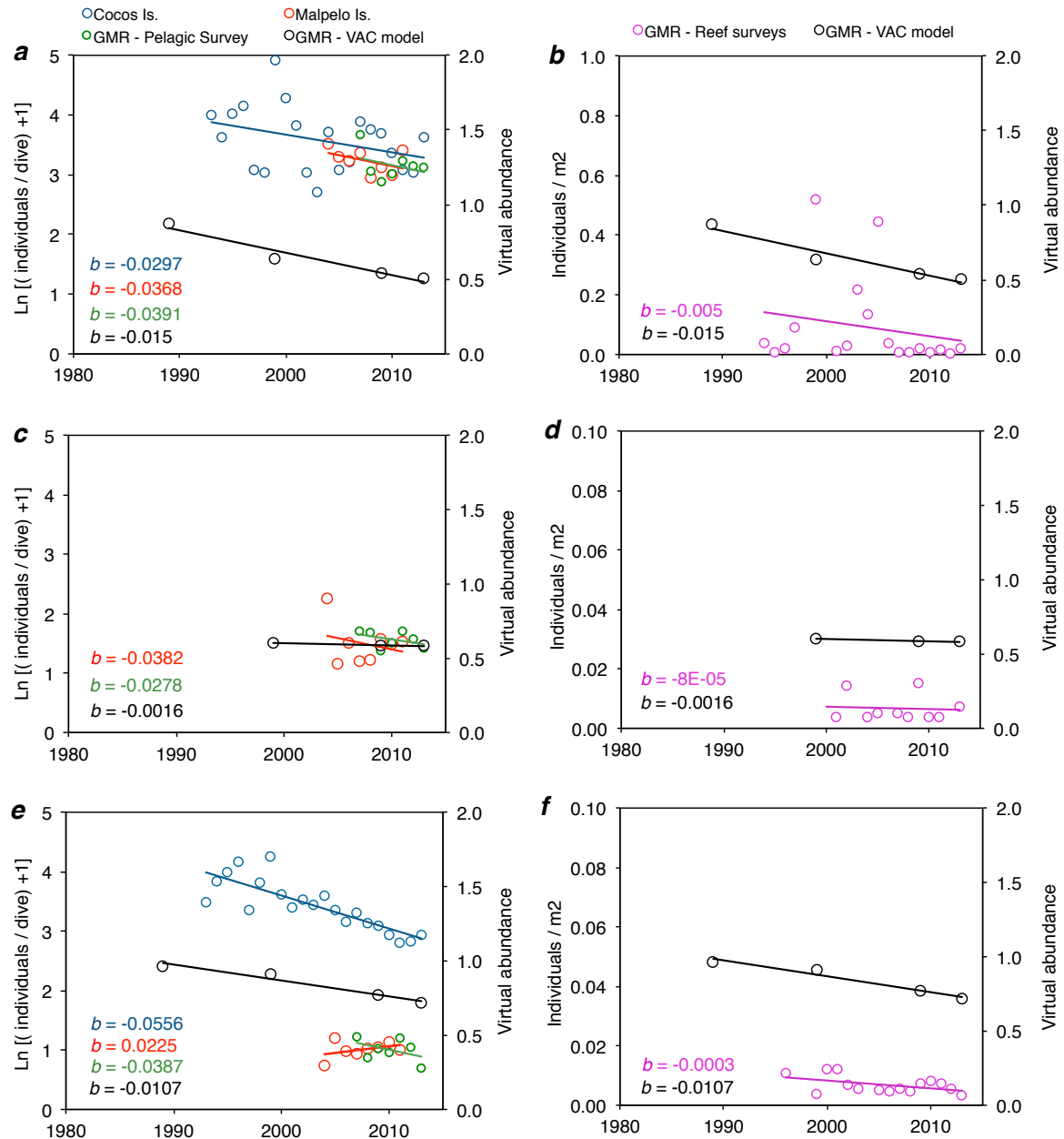
The relationship between perceived abundance change scores and the categorical trend scores per diver were used to estimate the values of the VAC model and the variance used to test the level of agreement (Figure 3.3). The whale shark was the only species perceived to be relatively stable across time. All other species showed a



considerable reduction in their perceived abundance. In the case of the hammerhead shark and whitetip reef shark, the reduction was steady across time. For the Galapagos shark and silky shark, the decline stabilized over the three most recent decades. For the blacktip shark, the reduction was followed by an increase in the virtual abundance toward the last two decades. The model shows silky sharks as the species with the least variance across decades, followed by the hammerhead and Galapagos sharks. The whitetip reef shark and whale shark had the narrowest variance during the first two decades, which steadily increased toward the last decade ( $s.d.= 0.38-0.5$ ). Finally, the blacktip shark had the highest variance across decades.



**Figure 3.3** Variation in the averaged virtual abundance change estimations across decades for the assessed shark species. Error bars represent the variability of each virtual abundance value based on the standard deviation of modelled answers; solid black line represents a fitted three-order polynomial regression trend line.



**Figure 3.4** Comparison of the VAC model linear trends for hammerhead sharks (a,b), Galapagos sharks (c,d) and whitetip reef sharks (e,f) with the linear trend of the natural logarithm of the abundances recorded by the Galapagos Pelagic Census Surveys (*GMR – Pelagic surveys*; Hearn A/CDF-UCD-DPNG, *unpublished data*), Galapagos Reef Fish Surveys (*GPS – Reef surveys*; Banks S./Charles Darwin Foundation, *unpublished data*); Cocos Island's shark abundance surveys ([White et al. 2015](#)) and Malpelo Island's shark abundance surveys ([Soler et al. 2013](#)). The  $b$  values represent the slope value of each trend line.

I used empirical datasets from fish monitoring programs in Cocos, Malpelo and Galapagos Islands to compare the VAC model results of hammerhead, Galapagos and whitetip reef sharks (Figure 3.4). In most cases the empirical datasets showed more pronounced negative trends than the VAC, although the slope of decline varied depending on the area, method and time period. For hammerhead sharks, the VAC trend was negative and similar in slope to the three fish monitoring datasets. The whitetip reef shark was also similar, with only the dataset from Malpelo showing a slightly positive trend. In contrast, the fish monitoring data for the Galapagos shark showed slightly negative trends, which differed from the stable trend obtained with the VAC model.

### **3.5 Discussion**

The identification of historical baselines is key in assessing whether changes in wildlife populations have occurred through time and to support assessments of their current population status ([Pauly 1995](#)). My analysis of the collective knowledge of divers in the GMR provided further evidence that formal data collection and monitoring can be supported by LEK as a viable method to evaluate population trends of iconic wildlife. I developed the semi-quantitative VAC analysis approach, as a rapid assessment tool of end-user's (diver's) perception of abundance trends without asking them to recall observed numbers of individuals. VAC estimates a decadal abundance indicator (termed virtual abundance) from the resulting change in abundance in previous decades instead of generating an average abundance score for each decade. I tested this approach for six shark species and identified four different shark trend scenarios that are congruent with biological surveys carried out in the

Galapagos and the ETP. The implications of these results in terms of model uncertainty and relevance for the management of the GMR are discussed below.

### **3.5.1 VAC approach and uncertainty**

LEK research is becoming a well-established scientific approach for the assessment of ecosystems and habitats ([Brook and McLachlan 2008](#)). Yet, because the approach is based on 'perceptions' it can be influenced by the natural decline in human memory ([Thompson 2000](#)). According to [Schacter \(2002\)](#) human memories can be affected by issues such as: *suggestibility*, when memories are implanted by others; *transience*, which refers to the retention of rare events of ecological salience; *misattribution*, when the feature under assessment (place or species) could be mistakenly allocated to a different time, spatial or intensity scale; and *individual bias*, in which the personal belief or perspective alters the memory of an event. To address these potential sources of bias, I took several considerations into account to reduce the uncertainty associated with LEK analyses.

Firstly, I used questionnaires to provide divers with simplified, standardized questions that could produce quantitatively comparable answers ([Huntington 2000](#)). This is a critical step necessary for the semi-quantitative analytical framework of the VAC tool. Questionnaires were designed to be self-guided and to have neutral, unpolarised questions that avoided influencing divers' responses with suggestions made within the text ([suggestibility bias, Schacter 2002](#)). Also, to avoid misattribution issues I designed the questionnaire to assess the six most common and charismatic shark species found in the GMR. Secondly, divers were selected in preference to fishermen to avoid potential bias from the controversial scenario linked to the exploitation of sharks in the GMR. It is critical to identify reliable LEK holders and

reduce potential individual bias, particularly if the final output of the LEK assessment could have controversial management implications ([van Putten et al. 2015](#)). Shark poaching ([Carr et al. 2013](#); [Reyes and Murillo 2007](#)) and controversial use of longline-fishing gears inside the GMR ([Altamirano and Aguiñaga 2002](#); [Ramírez and Reyes 2015](#)) could have compromised the results of this evaluation if fishermen LEK was explored. Thirdly, there were no records on the total number of divers who have worked in the reserve, increasing the risk of not properly identifying all the potential LEK holders. To support the adequacy of my final sample size, I included a peer-referral approach to identify all possible experienced divers, as suggested by [Huntington \(2000\)](#). My final sample size comprised the majority of people who were repeatedly named by interviewed divers, and was similar to other LEK studies that accurately described wildlife resource status (e.g. [Neis et al. 1999](#); [Yasué et al. 2010](#)). The lack of significant differences between the experience groups provided further support to consider divers a reliable source of LEK. Finally, to reduce potential issues of recalling events of ecological salience (transience bias), I asked divers to report the generalities (a perceived trend) rather than the particulars (yearly counts) of shark abundance. For example, asking divers about numerical abundances could have induced them to attempt complex mental calculations to remember and average the observed abundances. Such calculations could be likely influenced by the extreme (positive or negative) abundance conditions observed in major oceanographic events such as El Niño or la Niña (e.g. [Edgar et al. 2010](#); [Grove 1985](#); [Wolff et al. 2012b](#)).

In addition to this, humans have a natural tendency to assign the state of a resource they observed in the beginning of their careers/experience as baseline ([Pauly 1995](#)). The analysis of potential shifting base lines is critical to any historical trend reconstruction ([Ainsworth et al. 2008](#)), as different levels of experience among LEK

holders could produce negative ([Saenz-Arroyo et al. 2005](#)) or positive ([Roman et al. 2015](#)) changes in baselines. To ensure the abundance reconstruction of less experienced divers were consequent to those of more experienced divers, I incorporated a correction factor into my VAC model by adapting the approach of [Taylor et al. \(2011\)](#). I introduced this factor to estimate the remnant or surplus virtual abundance of each decade based on the perceived trend from previous decades. This approach was incorporated into the VAC model to produce a more realistic estimation of the continuous change in virtual abundance through decades, as suggested by [Ainsworth et al. \(2008\)](#).

While my approach attempted to provide a reliable reconstruction of virtual abundance and trends of sharks by considering the issues mentioned above, I did not obtain perfect agreement in the obtained categorical trend scores, and, consequently, in the VAC results (as shown by the standard deviations). Such degree of variation and accuracy is considered normal in light of the individual's belief, ability to recall events ([Bradburn 2000](#)), and to the heterogeneous distribution of the assessed species across their home range ([Crona 2006](#)). Similar variation in agreement has been previously reported in LEK studies assessing the population trends of birds ([e.g. Gregory et al. 2004](#)), bears ([e.g. Burghardt et al. 1972](#)), mountain lions ([e.g. Casey et al. 2005](#)), or biodiversity baselines ([e.g. Bunce et al. 2008](#); [Taylor et al. 2011](#)). For example, [Ainsworth et al. \(2008\)](#) assessed the abundance trends of keystone species using a comparable LEK analysis, and reported a variation up to two levels of magnitude in the fishermen's agreement. Their level of agreement was remarkably similar to that obtained in my VAC results, providing further support to the use of my methodology.

### 3.5.2 Validation of perceived trends

The validation process suggests VAC results provided reliable approximations of the population trends for the compared species, particularly for hammerhead sharks. This species' declining trend was consistent with the 45% reduction of abundance reported in Cocos Islands ([White et al. 2015](#)), 42% in Malpelo Islands ([Soler et al. 2013](#)), and in both GMR fish survey datasets. The reported decline of hammerhead sharks in fisheries across the ETP ([Baum et al. 2007](#)), along with wide ranging movements away from the reserve ([Ketchum 2011](#); [Ketchum et al. 2014b](#)), suggest the VAC results could be reflecting the population changes of this species both inside and in the surrounding waters of the GMR. In the case of whitetip reef sharks, the VAC result was similar to that from Cocos Islands and the GMR fish survey datasets, but not to Malpelo Island where the trend was described as rather stable ([Soler et al. 2013](#)). It is unclear what the causes of this decline may be within the GMR, particularly since whitetip reef sharks are coastal species with reduced mobility ([Barnett et al. 2012](#)), are not targeted by poachers ([Carr et al. 2013](#); [Reyes and Murillo 2007](#)), and are less susceptible to the local benthic fishing operations ([Peñaherrera and Hearn 2008](#)). It is possible that other mechanisms like predator-prey ecological interactions or tourism dynamics could be in play, and future research on these areas is needed to properly identify the underlining reasons of whitetip reef sharks perceived decline.

The observed LEK trend for Galapagos shark followed a declining pattern during the 1980s and 1990s, which then stabilized in the 2000s. I observed a disparity in the reported trends of Galapagos sharks in the region with my VAC data, particularly with the GMR Pelagic Surveys and [White et al. \(2015\)](#) datasets. For example, [White et al. \(2015\)](#) reported this species as generally infrequent in the dive sites of Cocos island

during early 1990s, yet its occurrence has steadily increased towards the 2010s. Contrastingly, the Malpelo dataset shows a negative trend across the 2000s, which also differs from [Soler et al. \(2013\)](#). These differences could be an artefact of the data standardization protocol used in my analysis, which presents the natural logarithm of the averaged annual abundance in contrast to the daily abundance data presented by [Soler et al. \(2013\)](#). However, these regional differences may be expected, given that Galapagos sharks display strong reef association ([Compagno et al. 2005](#)) and restricted mobility within the GMR ([Hearn et al. 2014](#)). The rather stable trend depicted by the VAC is consistent with the GMR Reef Fish surveys, which is the longest available abundance dataset for this species, suggesting a potential approximation to the trends of this species in Galapagos.

While there is no empirical dataset available to contrast the results for the other species in the GMR, the information from [White et al. \(2015\)](#) suggest the LEK results for blacktip and whale sharks may reflect the actual population trends for these species. Despite showing an increased variation in the standard deviation of results, the decadal averaged virtual abundance of the whale shark remained relatively stable since the 1980s. Compared to the other sharks assessed here, whale sharks display strong seasonality and site fidelity only in the north of the GMR ([Acuna-Marrero et al. 2014](#)), with sightings in other regions considered infrequent or even rare ([Hearn et al. 2014](#)). The amplitude in the decadal standard deviations could potentially reflect differences in seasonal experience among divers. Nevertheless, when summarizing the perception of all divers, the VAC model trend was similar to the trend reported from Cocos Islands ([White et al. 2015](#)). The Blacktip shark is the only species showing an increase in its virtual abundance in Galapagos. My data suggest this species may be experiencing a recovery after experiencing an abundance reduction of ~40% in the



1990's. Although no data from Malpelo Islands exists, the reported trend for Cocos Islands suggests an increase of 33% in the occurrence of this species during the last decade ([White et al. 2015](#)). The GMR is reported to be an important nursery ground for blacktip sharks ([Hearn et al. 2014](#)). The existence of such areas could be playing a significant role in the species' apparent recovery, especially since several of those sites are protected from extractive activities ([Llerena et al. 2015](#)).

During my analysis, I detected a possible misidentification issue between silky sharks and Galapagos sharks, given that both are similar in coloration, body shape and the first dorsal fin insertion ([Compagno et al. 2005](#)). While both species occur almost in the same habitats, divers do not often see silky sharks as they generally remain off the reef in open water areas. The large scale movements of silky sharks away from the GMR ([Hearn et al. 2014](#)), the importance of this species in artisanal ([Martinez-Ortiz et al. 2015](#)) and industrial fishing catches around the GMR ([Roman-Verdesoto and Orozco-Zoller 2005](#)), and the silky shark's global ([Bonfil 2009](#)) and regional population trends ([Soler et al. 2013](#); [White et al. 2015](#)), suggests an important disparity with rather conservative VAC estimates. Their movements away from the protection of the reserve makes them highly susceptible to industrial fishing operations ([IATTC 2010](#)). It is thus probable that this species is experiencing greater population reduction in the ETP, yet divers within the GMR has not accurately perceived it.

### **3.5.3 Implications for management and conservation of sharks**

Legal protection of sharks in the Galapagos Islands started in 1989 ([SRP 1989](#)), yet proper law enforcement started years later, especially after the creation of the GMR in 1998 ([Altamirano and Aguiñaga 2002](#)). Based on this, I expected divers to describe

positive trends in the abundance of coastal sharks as a result of the management framework of the GMR. Work on trophic webs suggested that the occurrence of the ENSO and the ban of the industrial fishing in 1998 might have allowed the biomass recovery of large predatory fishes, including large pelagic and coastal-pelagic sharks ([Wolff et al. 2012a](#)). I expected blacktip, Galapagos and whitetip reef sharks to show stable or positive trends, given that all their life stages and migratory movements have been reported to occur within the boundaries of the GMR ([Hearn et al. 2008](#); [Hearn et al. 2014](#)). However, my analysis suggests a contrasting scenario in which only blacktip sharks, and possibly Galapagos sharks, could be slowly experiencing the benefits of the reserve setting. Unexpectedly, the decline in whitetip reef sharks suggest this species might be subject to other mechanisms related to the internal management of the MPA and predator-prey ecological interactions, and conservation efforts should focus on understanding those aspects. Furthermore, I found no support for a positive effect of the reserve on the abundance of hammerhead sharks, which was suggested by [Wolff et al. \(2012a\)](#). The residency of hammerhead and silky sharks suggest those species use the reserve to some extent probably for feeding purposes, but it is still unclear if they use it to breed or as nursery grounds ([Hearn et al. 2014](#)). The GMR might be offering partial protection only for a certain stage of their lives, so they are still susceptible to the fishing operations outside the reserve and especially around its borders ([IATTC 2010](#); [WildAid 2010](#)). This is of concern for hammerheads, given they are endangered worldwide and conservation efforts currently in place may not prevent their decline in the ETP. Whale sharks' strong seasonality, short term residency ([Acuna-Marrero et al. 2014](#)) and vast migratory movements ([Hearn et al. 2013](#)) suggest the reserve offers little in terms of protection for this species. On this basis, the similarities of the assessed trends for hammerhead sharks, whitetip

reef sharks, and whale sharks between the GMR and the other MPAs suggests divers LEK may serve as an alternative indicator of their population status for the GMR.

Given the difficulties of assessing historical trends with conventional methods, I suggest my work should be complemented with genetic analysis on effective population size to understand the population dynamics of these species. Also, it is recommended that simple, low-cost methods of data collection (e.g. through citizen science or dive guides abundance logbooks) be adopted. These methods could greatly improve the quality of shark abundance data and provide more support regarding advantages and caveats of the VAC LEK approach. Despite being widely accepted that fisheries are the main drivers of shark decline worldwide ([Dulvy et al. 2014](#)), it is also important to compliment such species-specific studies with consideration of any changing environmental and anthropogenic conditions that could be affecting shark distributions around the reserve.

## **Chapter 4** *Home range and habitat preferences of the scalloped hammerhead shark Sphyrna lewini and the blacktip shark Carcharhinus limbatus in the Galapagos Marine Reserve*

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### **4.1 Abstract**

Spatial management through the implementation of marine protected areas is one strategy to limit the extraction of sensitive marine species. Yet, its use to protect wide ranging marine predators is still unproven, due to species' movements often exceeding the established boundaries of a protected area. Understanding the area used by marine life is thus a key step towards the evaluation of the management framework and efficacy of a protected area. To provide information of the protective coverage of the GMR, I assessed the habitat utilization distribution (UD) of hammerhead sharks and blacktip sharks in and around the GMR. Fifteen hammerhead sharks and 27 blacktip sharks were tagged with SPOT and SPLASH satellite tags in the north and south central regions of the GMR between 2007 and 2012. My results show important aspects of the extent and seasonality of the UD of hammerhead sharks and blacktip sharks inhabiting the GMR. Nearly 90% of hammerhead shark's UD was enclosed by the reserve boundary during the cold season (June-October), yet this progressively decreased to only ~30% with the advent of the warm season (December-April). Conversely, blacktip sharks' UD was 100% enclosed by the reserve boundaries in all seasons. Season and depth were the most important environmental parameters defining the core UD of hammerhead sharks; whilst year and eddy kinetic energy were the most important parameters for blacktip sharks. These findings suggest the size of the GMR may result in seasonally

variable protective coverage for sharks inhabiting either pelagic or coastal-pelagic environments.

## **4.2 Introduction**

Despite the controversy around the magnitude of species' declines ([Baum and Myers 2004](#); [Burgess et al. 2005](#)) and the ecological effect such declines may produce ([Grubbs et al. 2016](#); [Myers et al. 2007](#)), it is accepted that overfishing is the major cause of population decline among shark species ([Dulvy et al. 2014](#); [Ferretti et al. 2010](#)). Sharks are mostly caught as by-catch in fisheries targeting commercial teleost fish species, such as tuna and marlin ([Barker and Schluessel 2005](#)). As such, sharks are being harvested under management regulations more suited to species with higher intrinsic rebound potential ([Au et al. 2009](#); [Worm et al. 2013](#)). To avoid the collapse of shark populations, management should focus on reducing fishing mortality below sharks' natural population rebuilding rate ([Worm et al. 2013](#)). Managing fisheries to significantly reduce shark catches, or creating spatial closures, are the only available tools to halt the decline or recover shark populations ([Caddy and Agnew 2005](#); [Ward-Paige et al. 2012](#)).

The use of improved fishing gear ([Beverly et al. 2003](#)) and anti-finning legislation ([Gilman et al. 2008](#)) are important management regulations that can reduce the incidental capture of sharks ([Carlson et al. 2012](#)). Yet, the sustainable management of shark fisheries requires appropriate monitoring, assessment and enforcement of regulations, which is often resource-demanding ([Worm et al. 2013](#)). As such, managing shark fisheries becomes impractical in areas under the jurisdiction of undeveloped countries, or in international waters where the implementation of

regulatory fishing rules requires extensive and complex international agreements ([Barker and Schluessel 2005](#); [Hooker et al. 2011](#)).

Spatial management through the implementation of marine protected areas (MPA) is one strategy to limit the extraction of sensitive fish species and buffer the effects of fisheries in surrounding marine ecosystems ([Aburto-Oropeza et al. 2011](#); [Agardy 1994](#); [Claudet and Guidetti 2010](#)). There is substantial evidence supporting the implementation of MPAs in maintaining the biomass and diversity of coastal fish species (e.g. [Aburto-Oropeza et al. 2011](#); [Edgar et al. 2014](#); [Halpern 2003](#)), including coastal sharks ([Friedlander and DeMartini 2002](#); [Robbins et al. 2006](#)). Yet, the potential of MPAs to protect highly mobile species is still subject of debate (e.g. [Game et al. 2009](#); [Game et al. 2010](#); [Kaplan et al. 2010](#)). Shark movements can be larger in extension than MPA boundaries and national jurisdictions (e.g. [Block et al. 2011](#); [Hearn et al. 2013](#)), making them vulnerable when migrating to unmanaged open-fishing areas. If wide-ranging species are the management target, MPAs should encompass a significant proportion of their life stages and movements, with emphasis on reproducing adults ([Au et al. 2009](#)). Unfortunately, the lack of supporting evidence on the recovery of highly mobile fish species still limits a wider implementation of these reserves ([Ward-Paige et al. 2012](#)).

The Galapagos Marine Reserve (GMR) is the largest MPA in the Eastern Tropical Pacific Ocean (ETP), covering approximately 138000 km<sup>2</sup> of the pelagic environment surrounding the Galapagos Islands ([Danulat and Edgar 2002](#)). It lies in the confluence of three major currents that create complex oceanographic conditions, with marked seasonal gradients in current strength, sea surface temperature and productivity ([Palacios 2004](#)). The reserve was created in 1998 with the main aim of protecting all the coastal marine ecosystems and a significant proportion of the pelagic waters

surrounding the archipelago ([Danulat and Edgar 2002](#)). Theoretical approaches modelling the food-web interactions in the pelagic (open-water) Galapagos ecosystems, suggested that the pelagic and coastal-pelagic shark species would be expected to have increased in biomass since the creation of the GMR ([Wolff et al. 2012a](#)). However, by contrasting the ecological knowledge of dive guides against empirical information on the relative abundance of sharks, I showed that this apparent increase might only apply to certain coastal species, such as the blacktip shark (*Carcharhinus limbatus*) (this study, Chapter 3). Pelagic species such as the scalloped hammerhead shark (*Sphyrna lewini*) are reported to have declined by 50% in their relative abundance across the GMR (this study, Chapter 3). Given the unknown spatial scale of the home range of shark species around Galapagos, there are concerns the size of the reserve may not be adequate to protect sensitive species like the endangered scalloped hammerhead shark.

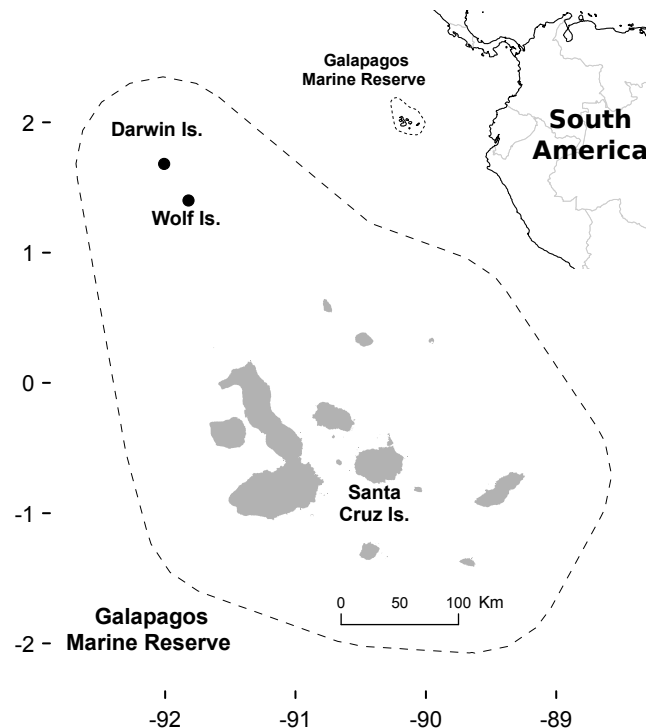
This study is aimed to assess the protective coverage of the GMR over the home range of the scalloped hammerhead shark and the blacktip shark. Specifically, I aimed to *i*) compare the environmental preferences of hammerhead and blacktip sharks in the GMR; *ii*) evaluate their spatial and temporal habitat utilization in relation to the size of the GMR; and *iii*) characterize the factors influencing the selection of core areas (preferred habitat) within their utilization distributions.

## **4.3 Methods**

### **4.3.1 Data collection**

The Galapagos Marine Reserve (GMR) is located approximately 1000 km east from the continental coast of Ecuador, South America (Figure 4.1). Field trips were carried

out from 2006 to 2014 to tag hammerhead and blacktip sharks in the north (Darwin and Wolf Islands) and south central (around Santa Cruz Island) regions of the GMR.



**Figure 4.1** Geographic location of the Galapagos Marine Reserve (GMR boundary: black line).

Ten hammerhead sharks were tagged in the north and five in the south central regions of the GMR between 2007 and 2012. Similarly, seven blacktip sharks were tagged in the north and 20 in the south central GMR between 2006 and 2014. All sharks were caught from a small boat using barbless circle hooks and nylon lines, with chunks of skipjack (*Katsuwonus pelamis*) or wahoo (*Acanthocybium solandri*) as bait. Once sharks were hooked, they were allowed to calm down on the line and then were slowly towed to a mother-vessel located less than 10 minutes away. Sharks were either brought on board using a sling and a hydraulic crane, or drawn onto a platform that was lowered into the water and subsequently raised above sea level. Once on the deck, sharks were immobilized, their eyes covered with a wet cloth, and



seawater was pumped continuously across their gills. Whenever a mother-vessel was not available, I approached the sharks via the side of the small boat, secured them with ropes, applied wet towels to their eyes, and pumped running seawater across the gills. All sharks were measured and sexed, after which satellite transmitters were attached to the dorsal fin with nuts and bolts. I used the fin-mount version of either SPOT 5 or SPLASH tags (Wildlife Computers – Redmond, USA). These tags were configured to opportunistically send location data to Argos satellites whenever a shark dorsal fin breached the water surface.

To eliminate inaccurate Argos satellite location information, I filtered out data using the package “argosfilter” ([Freitas 2012](#)) implemented within the R software environment ([R Core Team 2015](#)). Data was filtered to eliminate poor quality locations (Argos location classes [LC] B and A), values beyond sensor specifications (latitude and longitude), and unattainable speeds by animals greater than 2 ms<sup>-1</sup>, following [Weng et al. \(2007\)](#) and [Ketchum \(2011\)](#).

Filtered relocation data was then matched with physical oceanographic data using the Spatial Dynamics Ocean Data Explorer (SDODE) interface ([Hartog and Hobday 2011](#)). SDODE pairs the date and geographic location of each relocation of a shark trajectory with the date and grid cell of remote sensed oceanographic variable. The selected oceanographic variables were: sea surface temperature (hereafter SST) obtained from the NOAA’s Optimum Interpolated Sea Surface Temperature (0.25° x 0.25° resolution, ° Celsius) ([Reynolds et al. 2007](#)); Chlorophyll *a* data from the Moderate Resolution Imaging Spectroradiometer (Modis)-Aqua satellites (4 km · 8-day composite, mg/m<sup>3</sup>) ([Maccherone and Frazier 2015](#)); and the eddy kinetic energy (hereafter EKE) derived from the TOPEX / Poseidon and ERS-2 altimeters (0.2° spatial resolution, m<sup>2</sup>s<sup>2</sup>) ([Fu et al. 1994](#)). The EKE is a measure of the energy

associated with the turbulent flow of the ocean ([Wyrтки et al. 1976](#)). I complemented this data set by matching shark locations with the seafloor depth (hereafter depth) from a custom made bathymetric profile compiled from [Chadwick \(2001\)](#), [Peñaherrera-Palma et al. \(2013\)](#) and the 2-Minute Gridded Bathymetry and Global Relief Data (ETOPO2v2) ([Smith 1997](#)).

Tagging protocols were approved by the University of Tasmania Animal Ethics Committee (permit No. A13641), by the Institutional Animal Care and Use Committee of the University of California – Davis (permit number IACUC PROTOCOL #16022), and by the Directorate of the Galapagos National Park (research permit No. PC-60-13).

#### **4.3.2 Data analysis**

Habitat utilization was estimated by calculating the probability utilization distribution (hereafter UD) using the Brownian Bridge kernel method (BBKM) ([Bullard 1999](#); [Horne et al. 2007](#)) implemented in the “adehabitat” family package ([Calenge 2015](#); [Calenge et al. 2009](#)) within the R software environment. The BBKM is an extension of the classical kernel method that uses the properties of a conditional random walk between successive pairs of locations to place a bivariate normal probability density function over each movement step ([Bullard 1999](#)). The size and final orientation of the probability density function is dependent on two parameters: *i*) a first parameter defining the imprecision of each relocation; and, *ii*) a second related to the time and space travelled by the animal (called the Brownian Motion Variance factor) ([Horne et al. 2007](#)). To estimate the first parameter in my analysis, I used the mean error radius provided by the Argos satellite telemetry location information. I estimated the mean error radius for both species and seasons

separately. The Brownian motion variance parameter was then estimated by using a maximum likelihood approach developed by [Horne et al. \(2007\)](#). The analysis was placed in a grid system consisting of 25 km<sup>2</sup> cells around the GMR. The analysis was run per species and per season (cold: June-October, warm: December-April, transition: May and November). To test differences between the species' environmental preferences and UD areas, parametric (e.g. [Student's t-test, Gosset 1942](#)) and non-parametric tests (e.g. [Kruskal-Wallis test by ranks, Kruskal and Wallis 1952](#); [Mood's median test, Mood 1954](#)) were used.

The environmental preferences in probability of UDs of each shark species were assessed following [Papastamatiou et al. \(2013\)](#). First, I overlayed the UDs of all sharks of the same species, calculated the cumulative UD values per cell, and then transformed the cumulative UD to a fraction of 1 (by dividing each value by the maximum cumulative value obtained in the final grid). This particular analysis was aimed at characterizing the areas where all individuals from the same species coincided while migrating across the GMR. To evaluate this, a stepwise Generalized Additive Model (GAMs) was run using the UD as a response variable. GAMs were built under a Gaussian family distribution with identity links and smooth splines to model the single and additive effect of the predictive variables depth, SST, chlorophyll concentration, EKE, seasons and year. Model selection criteria were based on the adjusted Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) values to take into account differences in effective sample size and lack of fit ([Guisan et al. 2002](#); [Hastie and Tibshirani 1986](#)).

## **4.4 Results**

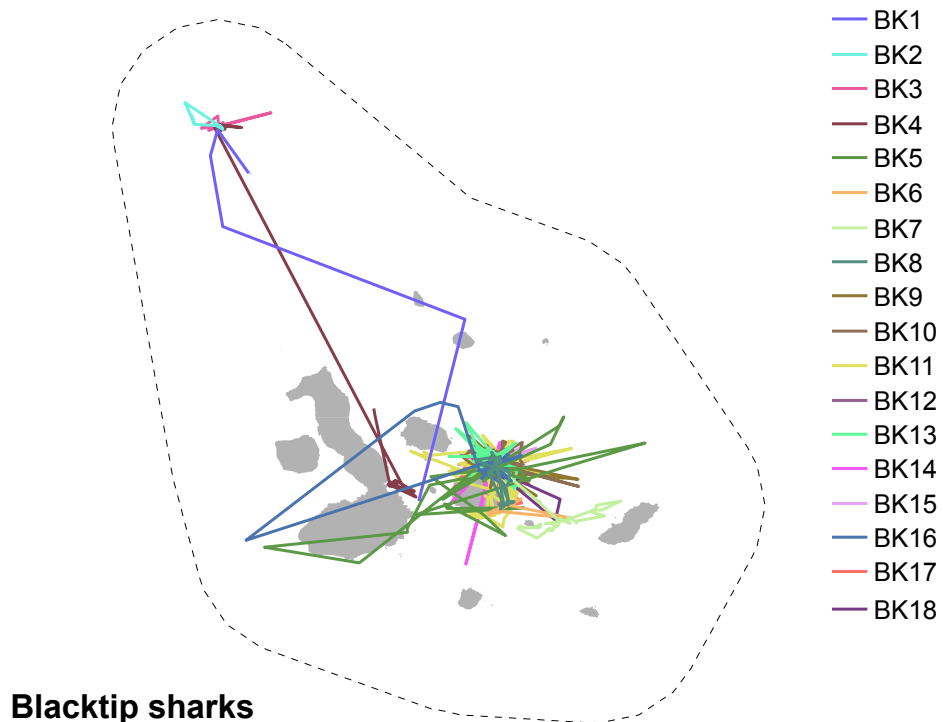
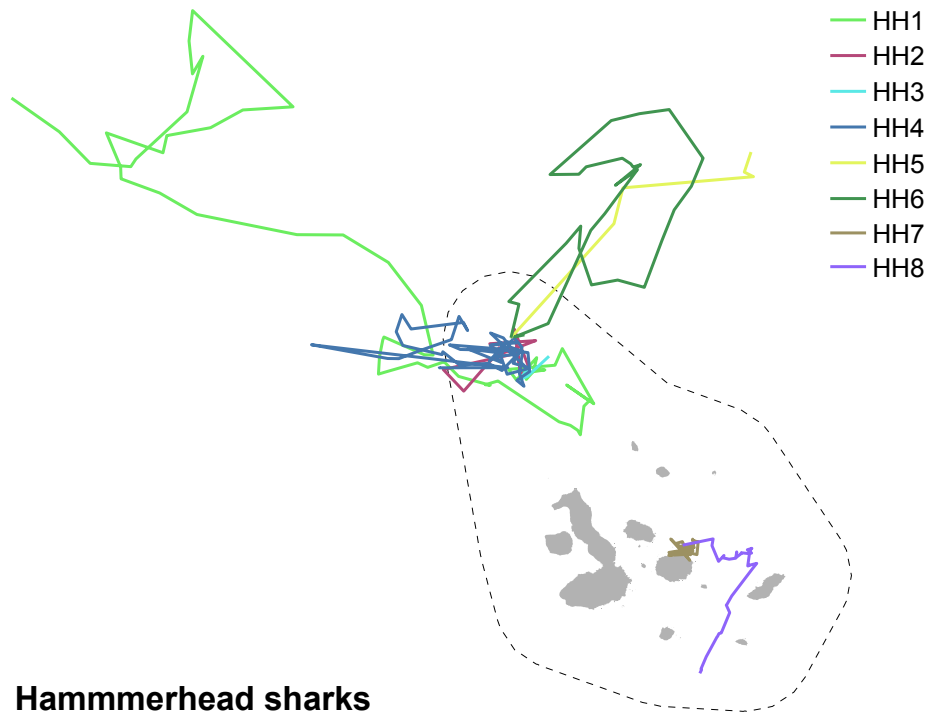
### **4.4.1 Summary of traversed trajectories**

Information was obtained from eight hammerheads (males=6, females =2) and 18 blacktip (males= 2, females=16) sharks (Table 4.1). The hammerhead sharks varied from 1.42 to 2.35 m in total length (mean = 1.97; SD= 0.34), with males being larger in size than females. The total number of transmissions per individual ranged between 5 and 91 (mean=37; SD=30) and the average time gap between successive relocations varied from 0.1 to 4.5 days (mean=2.2 days; SD= 1.6). Blacktip sharks ranged from 1.96 m to 2.54 m in total length (mean= 2.12; SD= 0.13). The total number of transmissions averaged 129.8, with a maximum of 422. The average time gap between successive relocations ranged from 0.4 up to 4.7 days (mean=1.3 days; SD= 1.1).

Hammerhead shark travel distance from the tagging location was significantly greater than that registered for blacktip sharks (t-test  $p=0.0044$ ). Individual hammerhead sharks covered a maximum distance of 586 km (mean=221 km, SD=191) from the tagging location, travelling to areas beyond the reserve boundaries (Figure 4.2). Blacktip sharks' maximum distance from the tagging location reached 292.7 km (mean= 73.7; SD=76.2), yet their movements were completely circumscribed by the reserve boundary, particularly north of Santa Cruz Island. Hammerhead sharks did not migrate between the north and south of the GMR, as was observed in two blacktip sharks.

**Table 4.1** Tracked scalloped hammerhead and blacktip sharks summary data. The averaged gap refers to the average time (in days) between two consecutive relocations. Distance from tagging site refers to the linear distance (in Km) between the tagging and the farthest location sharks travelled. Tagging bioregion: N, north; SC, south-central region.

Tag ID	Sex	Size	Tagging bioregion	Tagging date	Last transmission	Total days	Total transmission	Averaged gap (days)*	Distance from tagging**
<i>Hammerhead sharks</i>									
HH1	M	2.25	N	02-11-2007	26-01-2008	85	55	1.6	586.9
HH2	M	1.94	N	24-07-2008	16-09-2008	54	13	4.5	95.8
HH3	M	1.75	N	24-07-2008	07-08-2008	14	5	3.4	25.9
HH4	M	2.24	N	24-07-2008	19-12-2008	148	58	2.6	244.3
HH5	M	2.35	N	13-03-2009	01-04-2009	19	6	3.8	339
HH6	M	2.18	N	14-03-2009	20-04-2009	37	30	1.3	310.2
HH7	F	1.42	SC	13-12-2011	07-01-2012	25	91	0.3	21.6
HH8	F	1.6	SC	06-02-2012	11-02-2012	5	39	0.1	144.4
<i>Blacktip sharks</i>									
BK1	F	2.04	N	27-07-2006	16-08-2006	20	5	4.7	292.7
BK2	M	2.14	N	27-07-2006	16-08-2006	20	7	3	258
BK3	M	2.08	N	02-08-2006	26-08-2006	24	15	2	19.4
BK4	F	2.21	N	06-08-2006	22-10-2006	77	60	1.5	35.9
BK5	F	2.1	SC	26-11-2011	26-12-2011	30	38	0.8	73.4
BK6	F	2.15	SC	29-11-2011	19-12-2011	20	12	2.3	57.4
BK7	F	2	SC	18-12-2011	05-01-2012	18	40	0.5	87.9
BK8	F	2	SC	01-11-2013	01-12-2013	30	52	0.6	64.2
BK9	F	2.54	SC	26-01-2014	19-06-2014	144	249	0.5	23.5
BK10	F	2.03	SC	26-01-2014	07-08-2014	193	409	0.4	61.6
BK11	F	2.13	SC	28-01-2014	31-08-2014	215	422	0.5	74.6
BK12	F	2.03	SC	28-01-2014	30-03-2014	61	55	1.1	32.3
BK13	F	2.13	SC	28-01-2014	28-06-2014	151	221	0.7	60.8
BK14	F	2.15	SC	29-01-2014	10-05-2014	101	106	0.9	33.9
BK15	F	1.96	SC	31-01-2014	24-04-2014	83	172	0.5	58.1
BK16	F	2.29	SC	01-02-2014	13-03-2014	40	34	1.2	30.4
BK17	F	2.13	SC	01-02-2014	28-06-2015	512	288	1.7	37.5
BK18	F	2.03	SC	05-02-2014	21-05-2014	105	151	0.7	24.9



**Figure 4.2** Hammerhead sharks (above) and blacktip sharks (below) trajectories in and around the GMR. Black circles denote the locations cut-off where two tags (one hammerhead and one blacktip shark) started constant daily transmissions with high-speed movements ( $>2$  ms $^{-1}$ ) and linear trajectories.

#### 4.4.2 Environmental preferences

The traversed environmental conditions significantly differed between species (Table 4.2). In general, hammerhead sharks spent most time in waters with an average depth of 1560 m, SST of 25.1°C, relatively low chlorophyll *a* concentration (mean 0.336 mg m<sup>-3</sup>) and relatively high eddy kinetic energy (mean 132.2 m<sup>2</sup>s<sup>-2</sup>). Conversely, tagged blacktip sharks preferred areas with average depths of 140 m, SST of 25.7°, chlorophyll *a* concentrations of 0.682 mg m<sup>-3</sup> and eddy kinetic energy of 34.7 m<sup>2</sup>s<sup>-2</sup>. Seasonal environmental conditions also varied between individuals of the same species. In the case of hammerhead sharks, significant differences were obtained for all environmental variables except EKE (Table 4.3). This result was produced by an increased variability in the environmental conditions (depth, SST and chlorophyll) traversed by hammerhead sharks while moving away from the tagging locations during the warm season. Transition and colder season relocations were characterized by more stable environmental conditions. Despite most relocations from blacktip sharks being around Santa Cruz Island, the traversed environmental conditions per season significantly varied for all environmental variables (Table 4.3).

**Table 4.2** Global descriptive statistics (mean ± standard deviation) and significance tests (Kruskal-Wallis) of the differences in environmental preferences of satellite tracked hammerhead sharks (HHS) with blacktip sharks (BKT). Bold numbers indicate significant differences of  $p < 0.05$ .

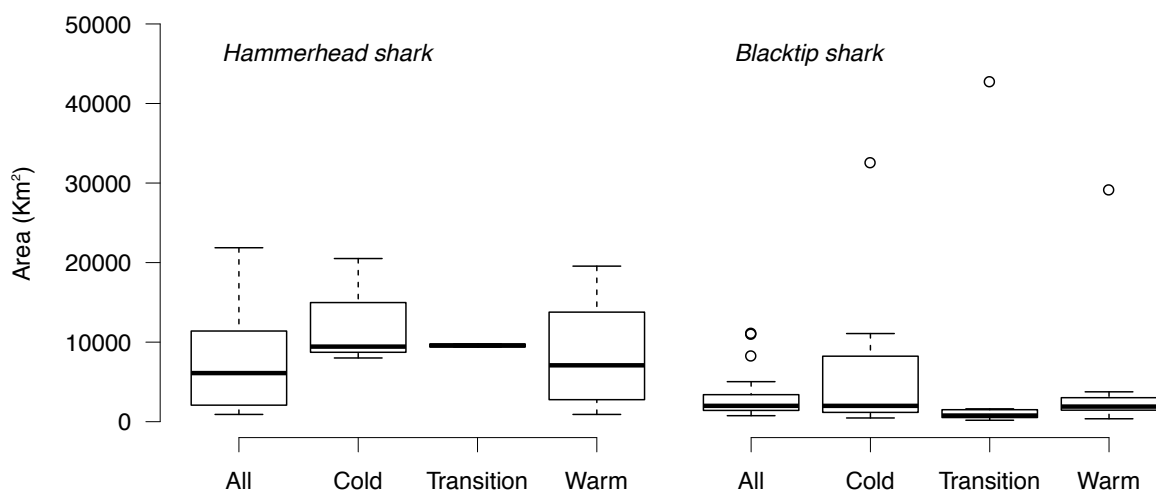
Species	Average ± S.D	Kruskal-Wallis X2	p
Depth			
HHS	-1581 ± 927	67.10	<0.01
BKT	-436 ± 268		
SST			
HHS	25.1 ± 1.8	344.10	<0.01
BKT	25.7 ± 1.2		
Chlorophyll			
HHS	0.336 ± 0.23	25.50	<0.01
BKT	0.682 ± 0.68		
EKE			
HHS	132.2 ± 190.8	14.70	<0.01
BKT	34.7 ± 15.5		

**Table 4.3** Summary descriptive statistics (mean  $\pm$  standard deviation) and significance tests (Kruskal-Wallis) of the seasonal environmental preferences of satellite tracked hammerhead sharks and blacktip sharks. Bold numbers indicate significant differences of  $p < 0.05$ .

		Seasons		Kruskal-Wallis	
	Cold	Transition	Warm	$\chi^2$	$p$
<i>Hammerhead sharks</i>					
Depth	-1937 ± 745	-2213 ± 546	-1371 ± 1017	25.80	<b>&lt;0.00</b>
SST	25.8 ± 0.6	24.4 ± 1.0	25.0 ± 2.0	23.30	<b>&lt;0.01</b>
Chlorophyll	0.248 ± 0.02	0.174 ± 0.02	0.341 ± 0.24	12.40	<b>&lt;0.01</b>
EKE	119.9 ± 134.4	66.7 ± 34.2	144.0 ± 213.1	2.60	0.26
<i>Blacktip sharks</i>					
Depth	-188 ± 455	-59 ± 184	-151 ± 299	62.00	<b>&lt;0.01</b>
SST	24.9 ± 0.9	25.7 ± 1.8	25.9 ± 1.1	467.70	<b>&lt;0.01</b>
Chlorophyll	1.497 ± 1.50	0.153 ± 0.15	0.483 ± 0.48	39.80	<b>&lt;0.01</b>
EKE	42.3 ± 30.4	33.0 ± 7.8	33.1 ± 9.7	11.10	<b>&lt;0.01</b>

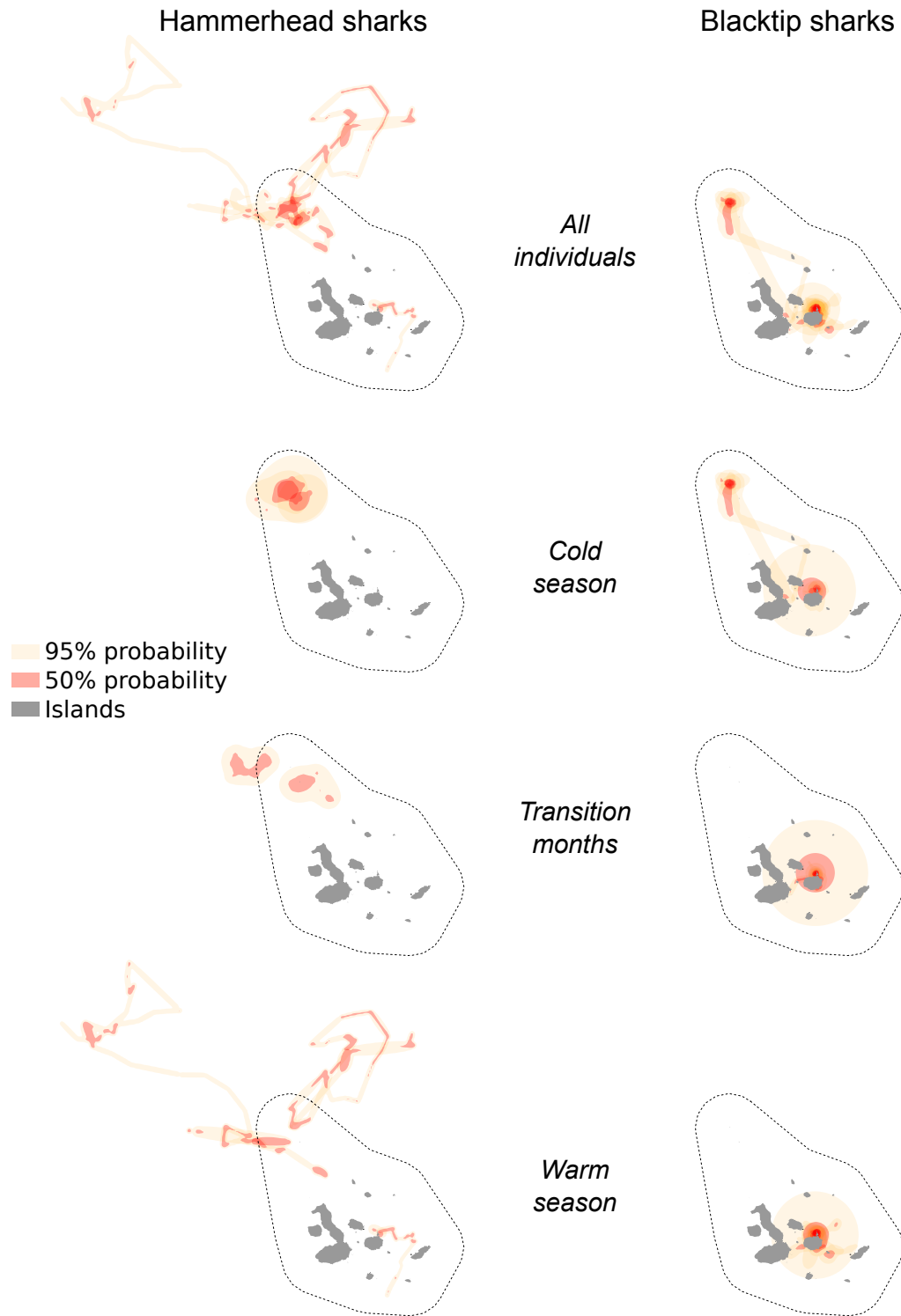
#### 4.4.3 Habitat utilization

The estimated UD area was significantly greater for hammerhead sharks than for blacktip sharks (Mood median test  $p < 0.01$ ; Figure 4.3). Hammerheads individual UD area varied from 912 to 21868 km<sup>2</sup> (median 6110), whilst blacktips' estimated UD area varied from 754 to 11155 km<sup>2</sup> (median 1993). Estimations of seasonal UD area did not yield significant differences within the same species (for hammerhead sharks, Mood test  $p > 0.74$ ; for blacktip sharks, Mood test  $p < 0.12$ ).



**Figure 4.3** Estimated area of utilization distribution of hammerhead sharks and blacktip sharks for *all* tracked individuals and between seasons (cold, transition and warm).





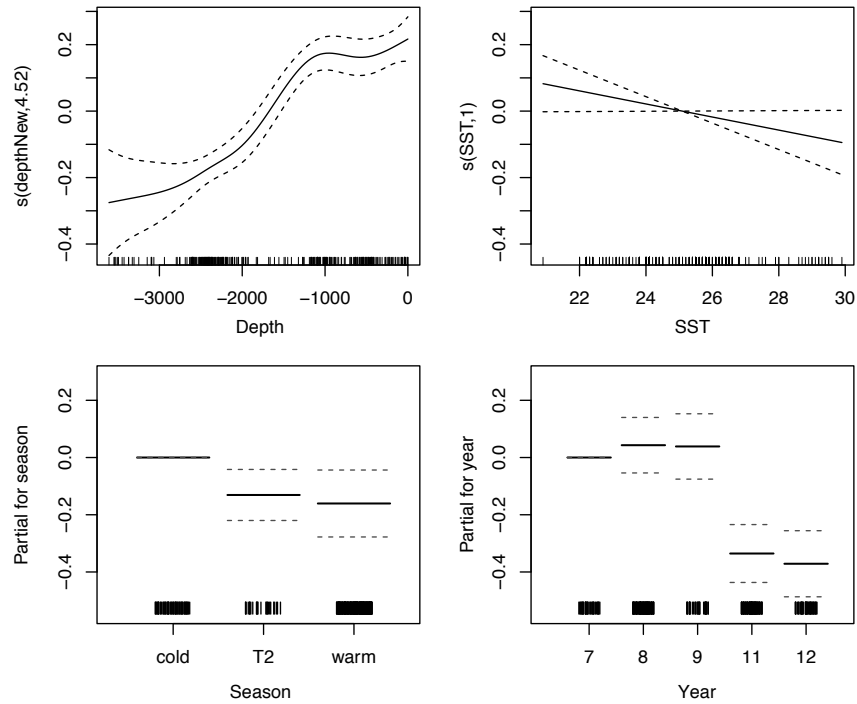
**Figure 4.4** Hammerhead sharks (*left column*) and blacktip sharks (*right column*) full tracks (top) and seasonal (middle and lower) utilization distribution areas in relation to the GMR boundary (dashed lines).

The area used by hammerhead sharks was confined around Darwin and Wolf Islands during the cold months, and extended away from the GMR boundaries in warmer seasons (Figure 4.4). Approximately 90% of the UD of hammerhead sharks was confined within the GMR during the cold season, 65% in the transition period, and 30% in the warm season. Conversely, blacktip sharks' UD was completely confined within the reserve across all seasons (Figure 4.4). Tagged blacktip sharks were more active and yielded larger UD areas during the colder months than in any other season (Figure 4.3 and 4.4).

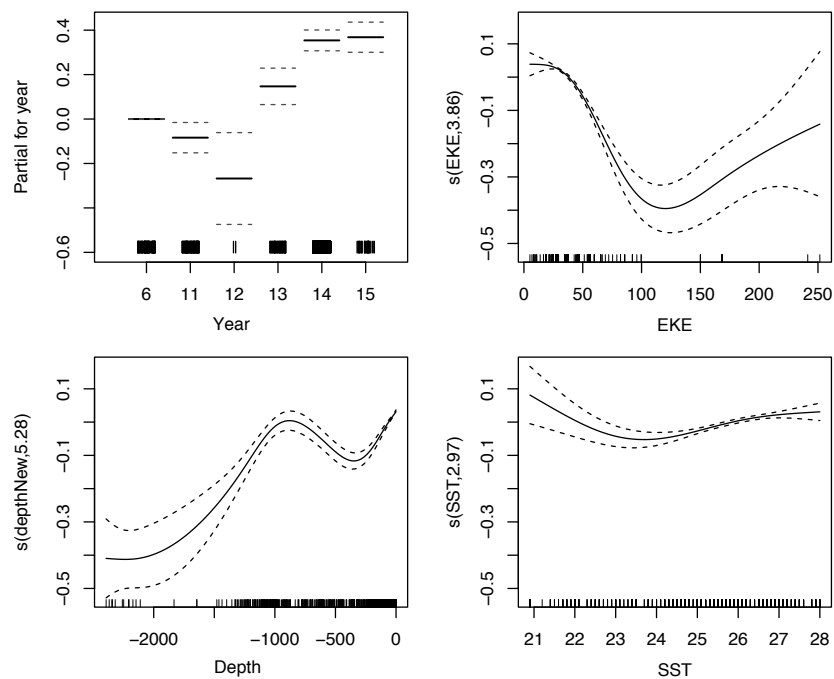
Season, year, depth and chlorophyll *a* were the only environmental predictors that statistically influenced ( $p < 0.01$ ) the probability of the UD of hammerhead sharks (Table 4.4). The best-fit model explained 51.7% ( $R^2$  0.493) of the total deviance and was obtained from the additive effects of depth, season, year and SST. Depth and season were the most important factors, followed by the year and SST. Despite the importance of chlorophyll *a* as a single factor, it did not have a major additive effect in the final model. Partial response curves suggest hammerhead sharks aggregate during the colder months (June – October) in areas shallower than 1000 m where SST is lower than 25°C (Figure 4.5). In the case of blacktip sharks, all environmental predictors had a statistically significant influence on their probability of UD, yet not all contributed to the top-fitted models (Table 4.4). The best-fit model for this species explained 64.7% ( $R^2$  0.493) of the total deviance and was built with four variables. Year and EKE were the most important factors influencing the model, followed by SST and season. Partial response curves suggest blacktip sharks were more active during 2006 to 2012, but stayed closer to the core UD area towards 2015. GAM results suggest that core UD area of this species is characterized by EKE lower than 50 m<sup>2</sup>s<sup>2</sup>, seafloor depth lesser than 500m and temperatures lower than 22°C (Figure 4.6).

**Table 4.4.** Model results from the generalized additive models for the effects of environmental covariates on the utilization distributions of hammerhead and blacktip sharks around the GMR. Chl: Chlorophyll *a*; SST: seas surface temperature; EKE, eddy kinetic energy; GCV: Generalized cross validation criteria. Stars (\*) indicate significant single predictors. Bold fonts, best fit models.

Model	AIC	BIC	Smoothing criterion	$R^2$	Explained deviance (%)
<i>Hammerhead sharks</i>					
One variable					
Season*	-191.7	-177.0	0.030	0.265	27.0
Depth*	-154.1	-121.8	0.035	0.179	19.8
Year*	-139.1	-117.0	0.036	0.128	14.0
Chl*	-134.2	-105.3	0.027	0.176	20.8
EKE	-106.7	-91.1	0.041	0.022	2.9
SST	-105.1	-89.0	0.041	0.016	2.4
Top models					
Depth + Season + Year	-289.1	-232.8	0.022	0.490	51.3
<b>Depth + Season + Year + SST</b>	<b>-289.7</b>	<b>-230.0</b>	<b>0.022</b>	<b>0.493</b>	<b>51.7</b>
Depth + Season + Year + EKE	-289.7	-228.7	0.022	0.494	51.9
Depth + Season + Year + SST +EKE	-290.0	-225.5	0.022	0.495	52.2
Full model	-213.6	-137.6	0.018	0.509	56.9
<i>Blacktip sharks</i>					
One variable					
Year*	-1979.0	-1938.7	0.025	0.495	49.6
EKE*	-1358.2	-1297.0	0.033	0.335	33.8
SST*	-990.2	-928.5	0.038	0.230	23.3
Depth*	-809.8	-770.1	0.041	0.167	16.9
Season*	-584.2	-561.2	0.046	0.082	8.2
Chl*	-328.2	-293.1	0.048	0.033	3.6
Top models					
Year + EKE + Depth	-2643.5	-2506.3	0.019	0.619	62.2
<b>Year + EKE + Depth + SST</b>	<b>-2764.8</b>	<b>-2579.3</b>	<b>0.018</b>	<b>0.639</b>	<b>64.4</b>
Year + EKE + Depth + Season	-2676.2	-2527.1	0.019	0.625	62.8
Year + EKE + Depth + SST + Season	-2782.0	-2584.8	0.018	0.642	64.7
Year + EKE + Depth + SST + Chl	-1906.3	-1724.3	0.018	0.643	65.0
Full model	-1924.6	-1724.8	0.018	0.632	64.0



**Figure 4.5** Generalized additive models (GAMs) showing the influence of depth, SST, season and year on the utilization distributions for all hammerhead sharks. Black tick marks above the x-axis represent the distribution of empirical data.



**Figure 4.6** Generalized additive models (GAMs) showing the influence of year, EKE, depth and SST on the utilization distributions for all blacktip sharks. Black tick marks above the x-axis represent the distribution of empirical data.

## 4.5 Discussion

Understanding the habitat utilization distribution (UD) of animals is a key step towards the evaluation of the management framework and efficacy of a protected area. My results show important aspects of the extent and seasonality of the UD of hammerhead sharks and blacktip sharks inhabiting the GMR. Nearly 90% of hammerhead sharks' UD was enclosed by the reserve boundary during the cold season (June-October), yet this progressively decreased to only ~30% with the advent of the warm season. Conversely, blacktip sharks' UD was 100% enclosed by the reserve boundaries in all seasons. Season and depth were the most important environmental parameters defining the presence of hammerhead sharks in the core areas of their UD. Year and EKE were the most important parameters for blacktip sharks. These results suggest the size of the GMR may have a seasonally variable protective coverage for sharks inhabiting either pelagic or coastal-pelagic environments.

### 4.5.1 Ecological aspects of utilization distribution

The scalloped hammerhead is found all year round in the GMR, particularly in higher relative abundance during the cold season (June-October) at the islands of Darwin and Wolf. [Klimley and Nelson \(1984\)](#) hypothesized this species uses the central refuging strategy ([Hamilton and Kenneth 1970](#)), by using oceanic islands and seamounts as a refuge, from where they can take advantage of nearby foraging areas. Long-term passive acoustic tracking has shown hammerhead sharks to display strong site fidelity to the islands of Darwin and Wolf ([Hearn et al. 2010](#); [Ketchum et al. 2014b](#)), which together with my study further supports the importance of both islands as a central-refuging area for hammerhead sharks. My results also suggest a

strong seasonal component in the use of the GMR by hammerhead sharks, with individuals progressively leaving the protection of the reserve with the advent of the warmer months. Hammerhead sharks' long distance migrations between MPAs of the ETP have been reported to occur also during the warm season ([Ketchum et al. 2014b](#)), yet it is still unknown which factors trigger such behaviour.

Pelagic species are known to change their geographic distribution between environmental seasons according to foraging, reproductive or parturition needs. For example, yellowfin and southern bluefin tuna shift their latitudinal distribution along the east coast of Australia in response to seasonal changes in the strength of the East Australian Current ([Hartog et al. 2011](#); [Hobday et al. 2010](#)). Dolphin species migrate along the Eastern Tropical Pacific Ocean following the seasonal shoaling of their preferred prey along thermocline ridges ([Reilly 1990](#)). The marked seasonality in the oceanographic setting of the GMR ([Palacios 2004](#)) could be playing a major role in the spatial extension of the UD in hammerheads around the GMR by influencing the vertical and horizontal distribution of their preferred prey items. The diet of adult hammerhead sharks is mostly comprised of cephalopod species like Humboldt squid ([Estupiñán-Montaña et al. 2009](#); [Loor-Andrade et al. 2015](#)), a species known to display climate-mediated range shifts ([Stewart et al. 2014](#)). [Bessudo et al. \(2012\)](#) reported the vertical behaviour of hammerhead sharks around Malpelo and Cocos Islands. Their study described hammerhead sharks undertaking deep "yo-yo" dives (>100 m) in waters away from the islands and during the warm season, whilst the same individuals mostly remained in surface waters (0-10m) near the islands during the colder season. In addition to foraging requirements, reproductive cues could also be driving hammerhead sharks away from the protection of the GMR. For example, female tiger sharks (*Galeocerdo cuvier*) tracked in the Hawaiian Archipelago also

display seasonal changes in distribution, mostly related to reproductive habitat preferences ([Papastamatiou et al. 2013](#)). Given that male hammerhead sharks drive gene flow dispersion, it is also possible that hammerheads departing from the GMR could do it in search of females to mate with. The lack reported nursery grounds within the GMR, and lack of genetic connectivity with identified nursery grounds on the ETP impossibilities this hypothesis to be tested.

Blacktip sharks are also a cosmopolitan species sharing similar distributions to hammerhead sharks among tropical and subtropical oceans of the world. There is a considerable amount of work available on the occurrence, demography and environmental preferences of juvenile blacktip sharks at nursery grounds in coastal and estuarine bays (e.g. [Froeschke et al. 2010](#); [Heupel and Hueter 2002](#); [Heupel and Simpfendorfer 2002, 2005](#); [Llerena et al. 2010](#)). Nevertheless, there is no available information regarding adult behavioural ecology, including UD. My study presents the first description on the UD of blacktip sharks while providing evidence of a potential hot-spot for this species. One study on fisheries records suggested that females might display site fidelity ([Dudley and Cliff 1993](#)). My results confirm this, with females (and two males) displaying a strong use of shallow areas (<500 m deep) in the centre of the south-central region of the GMR. These areas are mostly characterized by waters with low EKE due to the shadowing of the islands to horizontal oceanic currents. Why they display such a strong use of this area remains unclear. One possible explanation could be the proximity of the core UD to nursery areas for blacktip sharks found in the south central GMR ([Llerena et al. 2015](#)). The repeated seasonal use of the same nursery areas by female blacktip sharks has been reported at nursery grounds in the Northwest Atlantic, Gulf of Mexico and Caribbean ([Keeney et al. 2005](#)). In those areas, females remained close and used the same nursery

grounds, while males drove genetic differentiation and gene flow between populations. While there are no genetic analyses to corroborate this, several tracked females produced relocations within reported nursery grounds around Santa Cruz. The relationship between blacktip sharks using the reported core UD and the adjacent nursery grounds should be further explored.

Prey availability could also be playing an important role in habitat selection by blacktip sharks. An important breeding colony of the Galapagos sea lion (*Zalophus worrebaeki*) lies in Mosquera Islet (centre of blacktip shark core UD) ([Salazar 2002](#)), which is a suggested prey of blacktip and other similar-sized shark species ([Grove and Lavenberg 1998](#); [Villegas-Amtmann et al. 2008](#)). Other suggested prey items are whitetip reef shark *Triaenodon obesus*, which aggregate in areas near Mosquera Islet ([Grove and Lavenberg 1998](#)).

#### **4.5.2 Performance of the GMR with regard to sharks**

The GMR was created in 1998 to preserve its marine biodiversity and ecosystems from detrimental harvesting ([Danulat and Edgar 2002](#)). Unfortunately, at that time there was no information available on spatial behaviour and habitat preferences of any highly mobile species that could inform the reserve design. The selection of reserve size thus followed a precautionary approach to include all the coastal communities and a significant proportion of its pelagic surrounding ecosystems ([Danulat and Edgar 2002](#)). My results provide key information on the habitat selection and reserve use by hammerhead and blacktip sharks, with important implications regarding the reserve's protection coverage. For example, the spatial extent of the UD by blacktip sharks suggests the GMR might be providing coverage to a significant proportion of the spatial distribution of blacktip sharks. The spatial



distribution of identified nursery grounds of this species in the south-central region ([Llerena et al. 2015](#)), and the perceived recovery in the abundance expressed by divers (Chapter 3) further supports this, and suggest the GMR may be also providing protective coverage to different life stages of this species.

Unfortunately, the scenario for hammerhead sharks is less promising. My results suggest the GMR might only be providing sufficient protection during the cold season (months June-October). The UD of individuals during warmer months (December-April) suggest they are more susceptible to fishing operations around the reserve. Catch records from the Ecuadorean artisanal fishing fleet provides evidence of this, where hammerhead sharks were more commonly caught during the warm season and around the northern boundaries of the GMR ([Martinez-Ortiz et al. 2015](#)). Reserve size may not be adequately covering a significant proportion of the habitat of this species, which is of particular importance given its current global threatened status ([Baum et al. 2007](#)) and the reported regional decline in abundance ([Soler et al. 2013](#); [White et al. 2015](#); Chapter 3). Hammerhead sharks are highly susceptible to localized depletion due to their reduced gene flow and oceanic dispersal ([Duncan et al. 2006](#)), low potential to rebuild their populations ([Smith et al. 1998](#)) and elevated hooking mortality ([Gulak et al. 2015](#)).

Despite efforts to understand the behavioural and population ecology of this species in the GMR ([Hearn et al. 2014](#)), the importance of the reserve to its different life stages is still unknown. The smaller sizes of tagged individuals in the south central region, along with few records of neonates in mangrove-fringed bays ([Jaenig 2010](#); [Llerena 2009](#)), suggests the existence of nursery grounds for this species inside the GMR. A more in-depth analysis of this is required to determine the existence of such areas and review the protective coverage of the GMR to younger life stages of this

species. Also, although the seasonal patterns are highly probable, longer tracking would be needed to confirm this beyond reasonable doubt.

The inadequacy of the reserve size to protect hammerhead sharks has been previously reviewed based on connectivity mostly inferred from acoustic telemetry. [Ketchum \(2011\)](#) suggested the creation of several non-take MPAs enclosed in a large special marine managed area from Galapagos to Costa Rica. This special managed area would permit reduced fishing effort and should be equal in size to the Exclusive Economic Zones of the countries with national jurisdiction in the region. Increased reserve boundaries could be beneficial to protect this and other species but also the marine ecological corridors connecting the different MPAs in the region ([Shillinger 2005](#)). Achieving this complex spatial zoning, however, would require high levels of national and international agreements and would have important economic implications for the industrial fishing operations in the area. Also, this will not avoid interactions between fisheries and hammerhead sharks whenever they leave the small non-take MPAs. Alternatively, integrating temporary, mobile seasonal spatial closures extending the current fixed GMR boundaries could reduce the susceptibility of hammerhead sharks to fishing operations. Examples of this are currently in place to manage the longline fisheries on the east coast of Australia. The near real time dynamic spatial allocation of take and non-take areas reduces the interactions between the fishing fleets and pelagic by-catch species ([Hartog et al. 2011](#); [Hobday and Hartmann 2006](#); [Hobday et al. 2011](#)). This management approach could be applicable to create seasonal buffer zones and increase the extension of the reserve to reduce the capture susceptibility of hammerhead sharks. The reported seasonality in fisheries catches around the GMR by [Martinez-Ortiz et al. \(2015\)](#) supports the feasibility of this alternative. A further in-depth evaluation of the level of overlap

between catches of commercial teleost fishes and hammerhead sharks is recommended, particularly in neighbouring waters around the GMR. Also, habitat preferences of hammerhead sharks should be evaluated with a larger number of individuals per season, as recommended when assessing the implementation of dynamic spatial closures ([Hobday et al. 2010](#)).

The long-term spatial monitoring of sharks in the GMR should be maintained to better understand their temporal distributional patterns, and assess possible changes in response to major oceanographic events, such as el Niño Southern Oscillation. Furthermore, although the seasonal patterns depicted by my research are highly probable, longer tracking periods of hammerhead sharks would be needed to confirm this beyond reasonable doubt. Ensuring the long-term resilience of sharks is not only important due to their contribution in keeping the ecological balance of seamounts and pelagic communities, but also due to the economic importance they represent for the dive tourism industry in Galapagos ([Peñaherrera et al. 2013](#)).

## Chapter 5 *General Discussion*

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The main aim of this thesis was to assess the population trends and spatial extent of sharks inhabiting the Galapagos Marine Reserve (GMR) and generate decision-supporting tools to improve shark management at the local and regional level. Specifically, I assessed scalloped hammerhead shark (*Sphyrna lewini*) as a study case in contrast to other commonly occurring shark species in the GMR. This species was selected based on its global endangered status ([Baum et al. 2007](#)) and iconic importance for the marine tourism in the GMR ([Danulat et al. 2003](#)). Previous to this study, research efforts aimed at understanding the behavioural ecology of shark species within the GMR. There is still limited knowledge regarding their current and historical abundance trends. This was in part due to the lack of established long-term monitoring programs and appropriate evaluation tools. My work developed methodologies to assess population size and reconstruct historical trends by bridging several methodologies using population and behavioural ecology and the social sciences. My results provided the first estimates of resident population sizes for hammerhead sharks in the GMR while providing evidence of significant abundance decline during the last few decades. The status of this species contrasts with coastal shark species, which appear to be effectively protected by the GMR. To further understand the reasons for such decline, and frame the importance of the reserve to protect shark populations, I provided evidence that the GMR size does not adequately protect hammerhead sharks in comparison to coastal species. These findings, the questions they answer, and their research and management implications are discussed in the following sections.

## 5.1 Summary of findings

The evaluation of the population size of the scalloped hammerhead shark at Darwin Island, north of the GMR, is described in Chapter 2. To estimate the population size of this species I applied a novel mark-resight approach by combining acoustic telemetry and visual counts. In contrast to other methods, my approach used acoustic telemetry to build up the individual encounter histories, and reduced the effect of model assumption violation in terms of replacement and availability. Field trips of short duration (up to 10 days) were carried out at Darwin Island during the cold season months (September-October) to deploy acoustic tags and conduct underwater visual surveys (UVS). A total of 10, 21 and 20 individual sharks ranging from 190 to 285 cm in TL were marked with acoustic tags in 2011, 2012, and 2013, respectively. Females ranging from 160 to 280 cm in TL constituted almost 85% to 90% of the observed schools. Body size of the marked and observed individuals suggests that schools were mostly comprised of adult and sub-adult individuals.

Replacement (double counts) and availability (detected but unseen) ratios represented almost a quarter of the counted raw abundance. Yet their combined effect represented only a 2% variation in model estimates with negligible impact on the final results. Models provided strong evidence of time- and session-dependence in resighting probabilities and individual heterogeneity. This was particularly obvious in 2012, where the temporary emigration of marked and unmarked individuals affected the estimations of resident population ( $N^-$ ) and super-population size ( $N^*$ ) on some days. This generated more variable estimations with wider confidence intervals for 2012 ( $N^- \sim 642$  ind.;  $N^* \sim 1672$  ind.) in comparison to 2011 ( $N^- \sim 487$  ind.;  $N^* \sim 590$  ind.) and 2013 ( $N^- \sim 391$  ind.;  $N^* \sim 574$  ind.). Temporary emigration of

individuals becomes increasingly likely when assessing highly mobile species with gregarious behaviour and in a highly dynamic oceanographic setting.

The reconstruction of historical abundance trends of six shark populations from local ecological knowledge (LEK) is reported in Chapter 3. To assess this I developed a LEK-based virtual abundance change (VAC) model by using the ecological knowledge of divers working for the tourism industry. The model approach evaluates the decadal deficit or surplus in shark abundance since the beginning of the dive tourism industry in the 1980s. This approach does not require divers to make numerical estimations of observed abundance but to select a category trend (decline, stable or increase). Virtual population size was then inferred by asking divers to state their personal interpretation of these trend categories in numerical terms, from 0 to 100% of the population. Data was collected during several compulsory seminars held in 2013 by the Galapagos National Park.

Whilst dive guides showed consensus for negative trends for all shark species, my analysis depicted different perceived trends for each assessed species. Scalloped hammerhead sharks and whitetip reef sharks (*Triaenodon obesus*) experienced a consistent decline by 50% and 30%, respectively, over the last four decades. Silky sharks (*Carcharhinus falciformis*) and Galapagos sharks (*C. galapagensis*) were perceived to suffer an initial decline by 25% and 30%, respectively, yet later stabilized. Whale shark (*Rhincodon typus*) abundance was perceived as stable across the study, while blacktip sharks (*C. limbatus*) were the only species perceived to be experiencing abundance recovery after a 30% decline. My results were similar to empirical datasets from the GMR and other neighbouring marine protected areas (MPA) of the Eastern Tropical Pacific Ocean (ETP). These provided corroborating evidence that the dive guides' ecological knowledge has accurately described the

abundance fluctuations of all species except silky sharks. Fisheries, either legal or illegal, were suggested as the most important factor contributing to shark decline.

The evaluation of the habitat preferences and utilization distribution of hammerhead sharks to blacktip sharks is described in Chapter 4. To assess this I used satellite telemetry to evaluate sharks' environmental preferences, and estimate their core habitat based on their habitat utilization distribution (UD) modelled with the Brownian Bridge kernel method. Several fieldtrips were carried out from 2006 to 2014 to tag individual sharks at Darwin and Wolf Islands (north GMR), and around Santa Cruz Island (south-central GMR). A total of eight hammerhead sharks (males=6, females =2) and 18 blacktip sharks (males= 2, females=16) provided useful relocation information. This data showed that hammerhead sharks travelled significantly further from the tagging location (mean=221 km, SD=191) than those registered for blacktip sharks (mean= 73.7; SD=76.2; t-test  $p=0.0044$ ). Hammerhead sharks spent most time navigating in waters with an average depth of 1560 m, sea surface temperature of 25.1°C, relatively low chlorophyll *a* concentration (mean 0.336 mg m<sup>-3</sup>) and relatively high eddy kinetic energy (mean 132.2 m<sup>2</sup>s<sup>-2</sup>). Blacktip sharks preferred areas with average depths of 140 m, sea surface temperature of 25.7°, chlorophyll *a* concentrations of 0.682 mg m<sup>-3</sup> and eddy kinetic energy of 34.7 m<sup>2</sup>s<sup>-2</sup>.

The UD of individual hammerhead sharks displayed a strong seasonality in comparison to blacktip sharks. Nearly 90% of hammerhead sharks' UD was enclosed by the reserve boundary during the cold season (June-October), yet it progressively decreased to 65% in the transition months (May and November) and only a ~30% during the warm season (December-April). Conversely, blacktip sharks' UD showed no seasonal differences and was completely enclosed by the reserve boundaries. Generalized additive models revealed hammerhead sharks core UD is characterized

by waters shallower than 1000 m around Darwin and Wolf where SST is lower than 25°C. Blacktip sharks displayed a strong use of the waters north of Santa Cruz Island, particularly around Baltra Island. As such, their core habitat was characterized by waters of low eddy kinetic energy ( $<50 \text{ m}^2\text{s}^2$ ), seafloor depth shallower than 500m and sea surface temperatures lower than 22° C.

## **5.2 Significance of findings**

### **5.2.1 Methodological advances**

There are two important methodological advances in this study: *i*)the development of a telemetry-based mark-resight approach to assess population size of highly mobile fish species (Chapter 2); and *ii*)the development of a tool to assess the LEK of users in respect to the abundance of wildlife (Chapter 3). Both of these tools were critical in estimating historical and current abundance baselines for hammerhead sharks in the GMR.

The rigidity of previously available estimators ([McClintock and White 2012](#)) and the constraints of visually sighting marks in underwater conditions ([Griffing et al. 2014](#); [Zeller and Russ 2000](#)) have limited a wider application of mark-resight experiments in marine assessments. Through the use of telemetry to construct the re-sighting histories of marked individuals, I have provided an alternative experimental approach to deal with the issues of not sighting all available tags in underwater mark-resight experiments. Telemetry has been used to evaluate the sighting availability of terrestrial ([for a comprehensive revision see White and Shenk 2001](#)) and marine life ([Lee et al. 2014](#)) prior to carrying out the resight surveys. Alternatively, my approach only relies on visual observation to provide the total number of individuals in the



area, and uses telemetry as the only method to identify each mark from the observed group.

Model sensitivity was evaluated by using telemetry data to measure the effect of counting with replacement (over counting) and differential availability (under counting, individuals detected but not seen) in my estimations. My results provided evidence of over and undercounting bias cancellation, a situation also reported in the assessment of shark fisheries catch data ([Punt et al. 2000](#)), bull trout abundance from redd counts ([Dunham et al. 2001](#); [Muhlfeld et al. 2006](#)), haddock from experimental fishing ([Collie and Sissenwine 1983](#)), or mountain goats from aerial surveys ([Rice et al. 2009](#)). My approach was tested on the scalloped hammerhead shark population inhabiting Darwin Island, in the north of the GMR. Obtaining abundance estimates of wide-ranging shark species has proven to be problematic ([Griffing et al. 2014](#)). My modelling framework provided satisfactory estimations (with narrow confidence intervals) in two of the three fieldtrips carried out. Estimates for the remaining fieldtrip (2012) were affected by the temporary emigration of individuals, which is likely to naturally occur when assessing highly mobile species in variable environmental conditions ([Neal et al. 1993](#)). These results provide support to my findings and to use this new approach using telemetry and visual counts to evaluate the population size of highly mobile marine fishes. This approach should enable abundance estimates to be determined such that more quantitative and conclusive data can be generated for appropriate management.

The development of the LEK assessment tool, called VAC, was constructed to provide a proportional measure of abundance change that could be readily matched with the abundance data collected by the GMR Pelagic Fish surveys ([for full details on the monitoring program see Hearn et al. 2014](#)). This was partially possible due to the VAC

model design which *i)* required divers to select standardized trend categories without asking them to state numerical abundance estimations; *ii)* required divers to state how much (from 0 to 100%) every trend category meant to them; and *iii)* followed a cascade calculation approach to estimate the decadal virtual abundance instead of averaging the abundance scores per decade. These steps were central to provide the necessary semi-quantitative analytical framework of the VAC model, and to estimate decadal virtual abundances without any potential effect of cognitive shifting baselines among divers with different years of experience.

[Schacter \(2002\)](#) defines seven memory bias issues, from which four are particularly relevant to this LEK research: *suggestibility*, when memories are implanted by others; *transience*, which refers to the retention of rare events of ecological salience; *misattribution*, when the feature under assessment (place or species) could be mistakenly allocated to a different time, spatial or intensity scale; and *individual bias*, in which the personal belief or perspective alters the memory of an event. To increase the reliability of these results, I took several considerations into account to reduce the uncertainty associated with memory recalling. For example, I developed self-guided questionnaires with simplified, standardized questions that avoided influencing divers' responses ([suggestibility bias, Schacter 2002](#)). To reduce potential misattribution issues, study species were selected based on their charismatic profile, commonality and likelihood to be observed during any regular dive in the GMR. There was only one issue found regarding the ability of divers identifying between Galapagos shark and silky shark species; they are remarkably similar in coloration, body shape and first dorsal fin insertion ([Compagno et al. 2005](#)). While the validation process provided evidence of reliable results for the Galapagos sharks, there was an important disparity between my results, the global ([Bonfil 2009](#); [Clarke et al. 2006](#))

and regional declining trends ([Soler et al. 2013](#); [White et al. 2015](#)) of silky sharks. This misattribution issue precluded any conclusion on the validity of divers' LEK on regards of silky sharks.

The lack of a comprehensive database on the numbers divers who have worked in the reserve hampered the identification of all the potential LEK holders. To support the adequacy of my final sample size, a peer-referral approach was included to identify all possible LEK holders. This produced a final sample comprising the majority of people who were repeatedly named by divers, and similar to other LEK studies that accurately described wildlife resource status (e.g. [Neis et al. 1999](#); [Yasué et al. 2010](#)). To avoid any political and economic scenario affecting the answers of this evaluation ([Ruddle 2000](#)), I selected the reserve users (dive guides) without recorded conflicts regarding the management of the GMR ([Altamirano and Aguiñaga 2002](#)). By contrast, fishermen have historically been involved in issues regarding shark exploitation ([Carr et al. 2013](#)), which rises the uncertainty of obtaining reliable information. My selection of divers as LEK holders, and the obtained sample size is further supported by the lack of significant differences between divers with different levels of experience.

Despite these considerations, I obtained an important variation in the VAC standard deviations, evidencing different levels of agreement between divers. Similar LEK studies have reported varying levels of agreement when assessing the population trends of birds (e.g. [Gregory et al. 2004](#)), bears (e.g. [Burghardt et al. 1972](#)), mountain lions (e.g. [Casey et al. 2005](#)), or biodiversity baselines (e.g. [Taylor et al. 2011](#)). The variation in agreement is considered normal due to individual belief and ability to recall events ([Bradburn 2000](#)), and the heterogeneous distributions of species across their home range ([Crona 2006](#)). As such, this variability adds more value by

illustrating different viewpoints instead of one trend category induced by external factors.

### **5.2.2 Implications for the ecology of hammerhead sharks**

Through the application of a combined telemetry-visual counts approach, I have provided a fishery-independent alternative to the estimation of the population size of hammerhead sharks in an oceanic aggregation area (hot-spot). The closest comparable assessment was carried out more than 25 years ago in a seamount off the coast of Baja California, Mexico, by [Klimley and Nelson \(1981\)](#). They reported that hammerhead shark schools were formed by 12 to 225 individuals ranging from 1 to 3.4 m TL, and estimated a daily resident population size of 525 individuals. These values are comparable to those obtained in my research, where I counted from 0 to 380 individuals per dive, ranging from 1.6 to 2.4 m TL, and with daily resident population sizes averaging 546 (min=144, max=1656) individuals (this study, Chapter 2). Despite the methodological differences, the similarities of their estimation with my best-supported models provided an important comparative reference, and suggest the existence of potential constraints limiting the size of schools at oceanic islands and seamounts.

The constraints and how they limit the number of sharks in those aggregation areas have yet to be conclusively determined. The general consensus states carrying capacity is a function of the available food in a system ([Christensen and Pauly 1998](#)), yet hammerhead sharks are known to ignore the presence of potential prey when aggregating at oceanic islands and seamounts ([Klimley and Nelson 1984](#)). A possible explanation could rely on behavioural habitat selection. Theoretical modelling by [Krivan \(1998\)](#) proposed that refuge systems with strong, limited density provide

more stable interactions between predator and prey in adjacent habitats with no density constraints. It is possible that hammerhead sharks' habitat selection (open or refuge) could resemble that of a prey in Krivan's theory to maintain low densities in the refuge. Evidence of hammerhead sharks using oceanic islands and seamounts as a central refuging system have been provided by [Klimley and Nelson \(1984\)](#), [Hearn et al. \(2010\)](#), [Ketchum et al. \(2014a\)](#), [Ketchum et al. \(2014b\)](#), and are further supported by my results from Chapters 2 and 4. First, [Hearn et al. \(2010\)](#) and [Ketchum et al. \(2014a\)](#) provided evidence of back and forth excursions into open waters and a marked preference for the up-current areas of Wolf Island. Second, my results (Chapter 4) showed a clear island-centred core utilization distribution around Wolf and Darwin Island at least during the cold season (June-October). Third, acoustically tagged hammerhead sharks generated very low resighting probability values (0-0.3 this study, Chapter 2), suggesting that despite all sharks being in the area they never gathered all together at the same time at the study site. Finally, my best-supported abundance estimations (years 2011 and 2013, Chapter 2) show that hammerhead shark resident population size averaged between 400 to 600 individuals. Given the resemblance of the above-described behaviour and the modelled refuging system described by [Krivan \(1998\)](#), it is possible that the schooling and refuging of hammerhead sharks is an evolutionary response to predatory pressure by other extant and extinct marine fauna. Although there is evidence of predation upon hammerhead sharks by large predatory marine megafauna (e.g. by killer whales, [Soriso et al. 2006](#); [Visser and Bonaccorso 2003](#)), the extent of an evolutionary predatory pressure on hammerhead sharks is difficult to evaluate.

A further revision of the mechanisms defining the carrying capacity of an aggregation hot-spot is recommended, to assess what effects they have on overall population size

in the north of the GMR. A limited carrying capacity in these areas could signify increased susceptibility to depletion, since females constituted nearly 90% of the population sampled at Darwin Island (this study, Chapter 2). Females are the most important portion of a population, and should be protected with greater emphasis to avoid the species' collapse ([Au et al. 2009](#)). This is of special conservation concern given that this species has declined by 50% in the last 30 years (Chapter 3). Fisheries at these aggregation hot-spots could considerably affect the resilience of this species, and could be the underlining reason for the unrecovered and depleted state of hammerheads sharks reported by [Baum et al. \(2007\)](#) at the seamount firstly studied by [Klimley and Nelson \(1981\)](#).

### **5.2.3 Implications for the management of the GMR**

The Galapagos Archipelago is known to have historically held a large shark biomass ([Edgar et al. 2014](#); [Shimada and Shaefer 1956](#)). Previous to the creation of the GMR in 1998, hammerhead and other shark species were heavily targeted for their fins by national and international industrial fishing fleets ([Camhi 1995](#); [Camhi and Cook 1994](#); [Merlen 1995](#)). Concerns about shark status and the efficacy of the GMR were raised by divers and scientists ([Hearn et al. 2008](#); [Zarate 2002](#)), in response to constant shark poaching occurring around the reserve ([Carr et al. 2013](#); [Reyes and Murillo 2007](#)). While those events exposed the need for a revision of the population status of sharks, the lack of long-term monitoring programs in Galapagos has hampered the assessment of shark population response to the historical fishing pressure and later adopted management frameworks.

The findings in my thesis bring forward further conservation concerns on the efficacy of the GMR to protect coastal-pelagic shark species such as the scalloped

hammerhead shark. The low density in aggregation hot-spots (Chapter 2), the reserve-wide population decline (Chapter 3), seasonal movements beyond the reserve boundaries (Chapter 4), and the unknown presence of established nursery grounds ([Hearn et al. 2014](#)) suggest the GMR might not be providing enough protection for the populations of scalloped hammerhead sharks. Similar scenarios have been reported at Cocos and Malpelo Islands, neighbouring MPAs to the GMR in the ETP. In both areas, hammerhead shark movements were consistently larger than reserve size ([Bessudo et al. 2012](#)), and populations were reported to have declined by 50% in the last two decades ([Soler et al. 2013](#); [White et al. 2015](#)). Their findings are remarkably similar to this study, suggesting the GMR does not have an overall positive effect on hammerhead sharks suggested by the models by [Wolff et al. \(2012a\)](#). It is probable that the industrial fishing operations in the region could be the underlining reason for hammerhead shark decline inside these MPAs. This species is often caught by industrial ([IATTC 2010](#)) and artisanal ([Martinez-Ortiz et al. 2015](#)) fisheries operating around the reserve. The seasonal and spatial use of the reserve suggests hammerhead sharks are only protected at certain times of the year, particularly during the cold season (June-October; Chapter 4). The seasonality in the occurrence of hammerhead sharks observed in catch records from the Ecuadorean artisanal fishing fleet around the GMR ([Martinez-Ortiz et al. 2015](#)) provides further evidence of this.

The evaluation of hammerhead sharks raises concerns for the reserve's efficacy on other coastal-pelagic and pelagic shark species with similar life history traits. For example, silky sharks are coastal-pelagic species with no reported nursery grounds in the reserve, high-fidelity to certain areas within the reserve, and yet capable of broad scale movements away from the GMR ([Hearn et al. 2014](#)). If this species is not

breeding inside the reserve, its movements outside the reserve boundary make them more susceptible to overfishing by artisanal ([Martinez-Ortiz et al. 2015](#)) and industrial fisheries ([Roman-Verdesoto and Orozco-Zoller 2005](#)). Under this scenario, it is unknown to what extent the GMR will provide protection to coastal-pelagic or pelagic shark species. A further revision of this scenario is recommended, particularly to assess if any critical life stage is occurring inside the reserve. This will provide important insights into how to further improve the reserve management in relation to critical habitats for coastal-pelagic and pelagic species.

However, my findings suggest that the GMR may be adequate for protecting large coastal shark species with high levels of residency, such as the blacktip and Galapagos sharks (Chapter 3 and 4). This situation is possibly related to the reserve use of both species. For example, the habitat utilization distribution of blacktip sharks is enclosed within the reserve boundary throughout the year (Chapter 4). Their movements were particularly concentrated around Santa Cruz island, where important nursery grounds have been reported for this species ([Llerena et al. 2015](#)). While there is less data for Galapagos sharks, preliminary findings also suggest this species remains inside the GMR boundary in coastal areas near the islands ([Hearn et al. 2014](#)). As such, the analysis of historical baselines for this species suggests populations have been relatively stable since the 1990s, or even in potential recovery as perceived for the blacktip shark (Chapter 3). Similar trends have also been observed at Cocos Islands ([White et al. 2015](#)) and Malpelo Island ([Soler et al. 2013](#)). The reports provide further support that the GMR provides adequate coverage and protection for Galapagos, blacktip and other similar large coastal shark species.

Unexpectedly, the perceived decline in whitetip reef sharks raises questions as to whether this species is experiencing a negative rather than positive effect of the



creation of the reserve. This species is not targeted by poachers in Galapagos ([Carr et al. 2013](#); [Reyes and Murillo 2007](#)), and is less susceptible to the local coastal fishing operations ([Peñaherrera and Hearn 2008](#)). It is possible that other mechanisms like predator-prey ecological interactions or tourism dynamics could be in play. For example, the biomass of small sized-predator species is modelled to decline in response to an increase in biomass of larger predatory fish in the GMR ([Wolff et al. 2012a](#)). Important predators of whitetip reef sharks are tiger sharks, Galapagos sharks and possibly blacktip sharks ([Randall 1977](#)), all naturally occurring in coastal areas of the GMR ([Grove and Lavenberg 1998](#)), and all possibly experiencing positive effects of reserve setting (Chapter 3). Also, excessive use of diving sites by the tourism industry could also affect the observed abundance. Whitetip reef sharks were reported to avoid approaching divers in at least 45% of encounters ([Cubero-Pardo et al. 2011](#)). The decline of whitetip reef sharks could therefore either be a result of increased predation from larger shark species, and/or by habitat displacement to avoid encounters with divers or large predators.

### **5.3 Management recommendations and future studies**

Currently, there are important advances in the implementation of a special no-take zone around Darwin and Wolf islands, inside the northern portion of the GMR. While artisanal fisheries are allowed inside the GMR, the special no-take zone could reduce the pressure from artisanal fisheries in that area, and provide further protection to the reproductive populations of hammerhead sharks while foraging in the north of the reserve. It is recommended to further expand the evaluation of the population size of hammerhead sharks to include both Darwin and Wolf as a single unit of analysis. The newly developed methods will allow to estimate a baseline of the

population size in the north of the GMR, which is essential to review the effect of implementing the no-take zone around both islands. While estimations of population size can be carried out on an annual basis, the application of the VAC approach should be carried out in a timeframe no less than 5 years to allow users to perceive any potential population trend. In addition, the establishment of citizen science programs (e.g. by tourist or dive guide logs) will benefit resource evaluation by providing additional information on shark relative abundance and a comparable basis to the mark-resight and VAC methodologies developed through my research thesis.

Furthermore, while Darwin and Wolf Islands represent a critical foraging refuge habitat for female hammerhead sharks, it is strongly recommended that the importance of the south-central region for hosting early life stages of this species be reviewed. Protecting the areas used by hammerhead sharks in their early life stages, and the corridors connecting them with the no-take Darwin and Wolf area should complement this effort. This will allow the protection of different life stages occurring in the GMR but also the potential recovery of important historical aggregations of hammerhead sharks once found in the south-central region (Matthias Espinoza and Jonathan green, *pers. comm.*). A revision of the importance of the south-central region for other shark species is also recommended, as these areas could be a potential aggregation hot-spot for blacktip sharks as reported in Chapter 4.

It is important to note that any conservation inside the reserve should be complemented with long-term monitoring and research focused on diminishing the vulnerability of hammerhead sharks to fisheries operating outside the GMR, especially within the marine corridors between Galapagos, Cocos and Malpelo Islands. The implementation of dynamic spatial zoning should be reviewed to reduce the area overlapping between their core habitat and fisheries. Such zones may be

most important during warmer months when these sharks are less tied to the reserve area. Examples of such dynamic fishing zones are discussed by [Hobday et al. \(2010\)](#). This project contributes to the management of the GMR by providing baseline population ecological data and evaluation tools that can be easily applied to monitor the implementation of new management strategies. The developed methods in this study can be easily transferred to the assessment of any aggregation hot-spot of hammerhead sharks, or other fish species with similar behavioural traits.

## References

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- Abascal, F.J., Quintans, M., Ramos-Cartelle, A., Mejuto, J., 2011. Movements and environmental preferences of the shortfin mako, *Isurus oxyrinchus*, in the southeastern Pacific Ocean. *Marine Biology* 158, 1175-1184.
- Aburto-Oropeza, O., Erisman, B., Galland, G.R., Mascarenas-Osorio, I., Sala, E., Ezcurra, E., 2011. Large recovery of fish biomass in a no-take marine reserve. *PLoS One* 6, e23601.
- Acuna-Marrero, D., Jimenez, J., Smith, F., Doherty, P.F., Jr., Hearn, A., Green, J.R., Paredes-Jarrin, J., Salinas-de-Leon, P., 2014. Whale shark (*Rhincodon typus*) seasonal presence, residence time and habitat use at Darwin Island, Galapagos Marine Reserve. *PLoS One* 9, e115946.
- Agardy, T., 1994. Advances in marine conservation: the role of marine protected areas. *Trends in Ecology and Evolution* 9, 4.
- Ainsworth, C.H., Pitcher, T.J., Rotinsulu, C., 2008. Evidence of fishery depletions and shifting cognitive baselines in Eastern Indonesia. *Biological Conservation* 141, 848-859.
- Aldebert, Y., 1997. Demersal resources of the Gulf of Lions (NW Mediterranean). Impact of exploitation on fish diversity. *Vie et Milieu* 47, 275–285.
- Altamirano, M.V., Aguiñaga, M., 2002. Control y respeto al marco jurídico. In: E. Danulat, G.J. Edgar (Eds.), *La Reserva Marina de Galápagos. Línea Base de la Biodiversidad*. Fundación Charles Darwin y Parque Nacional Galápagos, Santa Cruz, Galápagos, Ecuador, pp. 459-473

- Amorim, A., Arfelli, C., Fagundes, L., 1998. Pelagic elasmobranchs caught by longliners off southern Brazil during 1974-97: an overview. . *Marine and Freshwater Research* 49, 621-632.
- Au, D.W., Smith, S.E., Show, C., 2009. Shark productivity and reproductive protection, and a comparison with teleosts. In: M. Camhi, E.K. Pikitch, E.A. Babcock (Eds.), *Intrinsic rates of increase in pelagic elasmobranchs*. John Wiley & Sons
- Banks, S., 2002. Ambiente Físico. In: E. Danulat, G. Edgar (Eds.), *Reserva Marina de Galápagos: Línea Base de la Biodiversidad*. Fundación Charles Darwin-Parque Nacional Galápagos, pp. 24-37
- Barbour, A.B., Ponciano, J.M., Lorenzen, K., O'Hara, R.B., 2013. Apparent survival estimation from continuous mark-recapture/resighting data. *Methods in Ecology and Evolution* 4, 846-853.
- Barker, M.J., Schluessel, V., 2005. Managing global shark fisheries: suggestions for prioritizing management strategies. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15, 325-347.
- Barnett, A., Abrantes, K.G., Seymour, J., Fitzpatrick, R., 2012. Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. *PLoS One* 7, e36574.
- Bartmann, R.M., White, G.C., Carpenter, L.H., Garrott, R.A., 1987. Aerial Mark-Recapture Estimates of Confined Mule Deer in Pinyon-Juniper Woodland. *The Journal of Wildlife Management* 51, 41-46.
- Baum, J., Clarke, S., Domingo, A., Ducrocq, M., Lamónaca, A.F., Gaibor, N., Graham, R., Jorgensen, S., Kotas, J.E., Medina, E., Martinez-Ortiz, J., Monzini Taccone di Sitizano, J., Morales, M.R., Navarro, S.S., Pérez-Jiménez, J.C., Ruiz, C., Smith, W., Valenti, S.V.,

- Vooren, C.M., 2007. *Sphyrna lewini*, In The IUCN Red List of Threatened Species. p. 2. International Union for the Conservation of Nature.
- Baum, J.K., Myers, R.A., 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters* 7, 135-145.
- Bennett, M.B., Gordon, I., Kyne, P.M., 2003. *Carcharhinus galapagensis*, In The IUCN Red List of Threatened Species. p. 2. IUCN 2015, Version 2015.2.
- Bessudo, S., Soler, G., Klimley, A., Ketchum, J., Arauz, R., Hearn, A., Guzmán, A., Calmettes, B., 2012. Vertical and Horizontal movements of the scalloped hammerhead shark (*Sphyrna lewini*) around Malpelo and Cocos Islands (Tropical Eastern Pacific) using satellite telemetry. *Boletín de Investigaciones Marinas y Costeras* 40, 91-106.
- Bessudo, S., Soler, G.A., Klimley, A.P., Ketchum, J.T., Hearn, A., Arauz, R., 2011. Residency of the scalloped hammerhead shark (*Sphyrna lewini*) at Malpelo Island and evidence of migration to other islands in the Eastern Tropical Pacific. *Environmental Biology of Fishes* 91, 165-176.
- Beverly, S., Chapman, L., Sokimi, W., 2003. Horizontal longline fishing methods and techniques. A manual for fishermen. Secretariat of the Pacific Community, Noumea, New Caledonia.
- Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.L., Ganong, J.E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W., Costa, D.P., 2011. Tracking apex marine predator movements in a dynamic ocean. *Nature* 475, 86-90.
- Bonfil, R., 2009. Chapter 10. The biology and ecology of the silky shark, *Carcharhinus falciformis*. In: M.D. Camhi, E.K. Pikitch, E.A. Babcock (Eds.), *Sharks of the open ocean: Biology, fisheries and conservation*. Published Online: 28 JAN 2009

- Bonfil, R., Amorim, A., Anderson, C., Arauz, R., Baum, J., Clarke, S.C., Graham, R.T., Gonzalez, M., Jolón, M., Kyne, P.M., Mancini, P., Márquez, F., Ruíz, C., Smith, W., 2009. *Carcharhinus falciformis*, In The IUCN Red List of Threatened Species. p. 2. International Union for the Conservation of Nature.
- Bradburn, N.M., 2000. Temporal representation and event dating In: A.A. Stone, J.S. Turkkan, C.A. Bachrach, J.B. Jobe, H.S. Kurtzman, V.S. Cain (Eds.), The science of self report: implications for research and practice. Lawrence Erlbaum Associates, Mahwah, New Jersey, USA, pp. 49–61
- Branstetter, S., 1987. Age, growth and reproductive biology of the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead shark, *Sphyrna lewini*, from the northwestern Gulf of Mexico. Environmental Biology of Fishes 19, 161-173.
- Brock, R.E., 1982. A Critique of the Visual Census Method for Assessing Coral Reef Fish Populations. Bulletin of Marine Science 32, 269-276.
- Brook, R.K., McLachlan, S.M., 2008. Trends and prospects for local knowledge in ecological and conservation research and monitoring. Biodiversity and Conservation 17, 3501-3512.
- Bullard, F., 1999. Estimating the home range of an animal: a Brownian bridge approach. Johns Hopkins University.
- Bunce, M., Rodwell, L.D., Gibb, R., Mee, L., 2008. Shifting baselines in fishers' perceptions of island reef fishery degradation. Ocean and Coastal Management 51, 285-302.
- Burgess, G.H., Beerkircher, L.R., Cailliet, G.M., Carlson, J.K., Cortés, E., Goldman, K.J., Grubbs, R.D., Musick, J.A., Musyl, M.K., Simpfendorfer, C.A., 2005. Is the collapse of shark populations in the Northwest Atlantic Ocean and Gulf of Mexico real? Fisheries 30, 19-26.

- Burgess, H.G., Branstetter, S., 2009. *Carcharhinus limbatus*, In The IUCN Red List of Citation: Threatened Species. IUCN 2015.
- Burghardt, G.M., Hietala, R.O., Pelton, M.R., 1972. Knowledge and attitudes concerning black bears by users of the Great Smoky Mountains National Park. In, Bears: Their Biology and Management. International Association for Bear Research and Management, pp. 255-273
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multinomial inference: A practical information-theoretic approach., Second Edition. edn. Springer-Verlag, New York, NY.
- Caddy, J.F., Agnew, D.J., 2005. An overview of recent global experience with recovery plans for depleted marine resources and suggested guidelines for recovery planning. Reviews in Fish Biology and Fisheries 14, 43-112.
- Cairns, J., Jr., McCormick, P., Niederlehner, B.R., 1993. A proposed framework for developing indicators of ecosystem health. Hydrobiologia 263, 1-44.
- Calenge, C., 2015. Home Range Estimation in R: the adehabitatHR Package. Office national de la classe et de la faune sauvage Saint Benoist – 78610 Auffargis – France.
- Calenge, C., Dray, S., Royer-Carenzi, M., 2009. The concept of animals' trajectories from a data analysis perspective. Ecological Informatics 4, 34-41.
- Camhi, M., 1995. Industrial Fisheries Threaten Ecological Integrity of the Galapagos Islands. Conservation Biology 9, 715-719.
- Camhi, M., Cook, S.F., 1994. Sharks in Galapagos in peril. Shark News 2.
- Camhi, M., Fowler, S., Musick, J.A., Brautigam, A., Fordham, S., 1998. Sharks and their relatives: ecology and conservation. Vol 20. Occasional Paper. The IUCN Species Survival Commission.



- Capello, M., Robert, M., Soria, M., Potin, G., Itano, D., Holland, K., Deneubourg, J.L., Dagorn, L., 2015. A Methodological Framework to Estimate the Site Fidelity of Tagged Animals Using Passive Acoustic Telemetry. *PLoS One* 10, e0134002.
- Carlson, J.K., Hale, L.F., Morgan, A., Burgess, G., 2012. Relative abundance and size of coastal sharks derived from commercial shark longline catch and effort data. *Journal of Fish Biology* 80, 1749-1764.
- Carr, L.A., Stier, A.C., Fietz, K., Montero, I., Gallagher, A.J., Bruno, J.F., 2013. Illegal shark fishing in the Galápagos Marine Reserve. *Marine Policy* 39, 317-321.
- Casey, A.L., Krausman, P.R., Shaw, W.W., Shaw, H.G., 2005. Knowledge of and Attitudes Toward Mountain Lions: A Public Survey of Residents Adjacent to Saguaro National Park, Arizona. *Human Dimensions of Wildlife* 10, 29-38.
- Castley, J.G., Knight, M.H., Mills, M.G.L., Thouless, C., 2002. Estimation of the lion (*Panthera leo*) population in the southwestern Kgalagadi Transfrontier Park using a capture–recapture survey. *African Zoology* 37, 27-34.
- Chadwick, B., 2001. Galapagos Bathymetry. Web page NOAA <http://newport.pmel.noaa.gov/~chadwick/galapagos.html>.
- Chambers, L.E., Patterson, T., Hobday, A.J., Arnould, J.P.Y., Tuck, G.N., Wilcox, C., Dann, P., 2014. Determining trends and environmental drivers from long-term marine mammal and seabird data: examples from Southern Australia. *Regional Environmental Change* 15, 197-209.
- Christensen, V., Pauly, D., 1998. Changes in Models of Aquatic Ecosystems Approaching Carrying Capacity. *Ecological Applications* 8, S104-S109.
- Cisneros-Montemayor, A.M., Barnes-Mauthe, M., Al-Abdulrazzak, D., Navarro-Holm, E., Sumaila, U.R., 2013. Global economic value of shark ecotourism: implications for conservation. *Oryx* 47, 381-388.

Clarke, S.C., McAllister, M.K., Milner-Gulland, E.J., Kirkwood, G.P., Michielsens, C.G., Agnew, D.J., Pikitch, E.K., Nakano, H., Shivji, M.S., 2006. Global estimates of shark catches using trade records from commercial markets. *Ecology Letters* 9, 1115-1126.

Claudet, J., Guidetti, P., 2010. Improving assessment of marine protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* 20, 239 - 242.

Collie, J.S., Sissenwine, M.P., 1983. Estimating Population Size from Relative Abundance Data Measured with Error. *Canadian Journal of Fisheries and Aquatic Sciences* 40, 1871-1879.

Compagno, L.J.V., Dando, M., Fowler, S., 2005. *Sharks of the world*. Princeton University Press, New Jersey, USA.

Cooch, E., White, G.C., 2014. Program Mark: "A gentle introduction", 11th edition. edn.

Cortés, E., 2000. Life History Patterns and Correlations in Sharks. *Reviews in Fisheries Science* 8, 299-344.

Crona, B.I., 2006. Supporting and Enhancing Development of Heterogeneous Ecological Knowledge among Resource Users in a Kenyan Seascape. *Ecology and Society* 11, 32.

Cubero, P., 2008. Plan de Monitoreo para evaluación del impacto del Ecoturismo Marino en las Islas Galápagos. Contexto Análisis de Indicadores y Protocolos de monitoreo, pp. 1-79. Asistencia Técnica, Fundación Charles Darwin, Puerto Ayora, Galápagos, Ecuador.

Cubero-Pardo, P., Herrón, P., González-Pérez, F., 2011. Shark reactions to scuba divers in two marine protected areas of the Eastern Tropical Pacific. *Aquatic Conservation: Marine and Freshwater Ecosystems* 21, 239-246.

Danulat, E., Brandt, M., Zarate, P., Montesinos, M., Banks, S., 2003. El turismo en la Reserva Marina de Galápagos. Análisis global y condiciones en sitios de visita marinos

seleccionados. Estación Científica Charles Darwin y Dirección Parque Nacional Galápagos, Puerto Ayora, Galapagos, Ecuador.

Danulat, E., Edgar, G., 2002. Reserva Marina de Galápagos. Línea Base de la Biodiversidad. Fundación Charles Darwin y Parque Nacional Galápagos, Santa Cruz, Galápagos, Ecuador.

Davidson, L.N.K., Krawchuk, M.A., Dulvy, N.K., 2015. Why have global shark and ray landings declined: improved management or overfishing? Fish and Fisheries, n/a-n/a.

Davis, A., Wagner, J.R., 2003. Who knows? On the importance of identifying "experts" when researching local ecological knowledge. Human Ecology 31, 463-489.

Denham, J., Stevens, J.D., Simpfendorfer, C.A., Heupel, M.R., Cliff, G., Morgan, A., Graham, R., Ducrocq, M., Dulvy, N.K., Seisay, M., Asber, M., Valenti, S., Litvinov, F., Martins, P., Lemine Ould Sidi, M., Tous, P., Bucal, D., 2007. *Sphyrna mokarran*, In The IUCN Red List of Threatened Species., p. 2. IUCN 2015.

Dennhardt, A.J., Duerr, A.E., Brandes, D., Katzner, T.E., 2015. Integrating citizen-science data with movement models to estimate the size of a migratory golden eagle population. Biological Conservation 184, 68-78.

Domeier, M.L., 2006. An analysis of Pacific striped marlin (*Tetrapturus audax*) horizontal movement patterns using pop-up satellite archival tags. Bulletin of Marine Science 79, 811-825.

DPNG, 2009. Se instaló el sistema para el monitoreo de embarcaciones en la DPNG, In Noticias. PR.C.P003.R002 - 2009-05-05 - No. 071. Dirección Parque Nacional Galápagos.

Dudgeon, C.L., Pollock, K.H., Braccini, J.M., Semmens, J.M., Barnett, A., 2015. Integrating acoustic telemetry into mark-recapture models to improve the precision of apparent survival and abundance estimates. Oecologia 178, 761-772.

- Dudley, S.F.J., Cliff, G., 1993. Sharks caught in the protective gill nets off Natal, South Africa. 7. The blacktip shark *Carcharhinus limbatus* (Valenciennes). South African Journal of Marine Science 13, 237–254.
- Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N., Fordham, S.V., Francis, M.P., Pollock, C.M., Simpfendorfer, C.A., Burgess, G.H., Carpenter, K.E., Compagno, L.J., Ebert, D.A., Gibson, C., Heupel, M.R., Livingstone, S.R., Sanciangco, J.C., Stevens, J.D., Valenti, S., White, W.T., 2014. Extinction risk and conservation of the world's sharks and rays. Elife 3, e00590.
- Duncan, K.M., Martin, A.P., Bowen, B.W., De Couet, H.G., 2006. Global phylogeography of the scalloped hammerhead shark (*Sphyrna lewini*), pp. 2239-2251. Blackwell Publishing Ltd.
- Dunham, J., Rieman, B., Davis, K., 2001. Sources and Magnitude of Sampling Error in Redd Counts for Bull Trout. North American Journal of Fisheries Management 21, 343-352.
- Eddy, T.D., Gardner, J.P., Perez-Matus, A., 2010. Applying Fishers' ecological knowledge to construct past and future lobster stocks in the Juan Fernandez Archipelago, Chile. PLoS One 5, e13670.
- Edgar, G.J., Banks, S., Fariña, J.M., Calvopiña, M., 2004. Regional biogeography of shallow reef fish and macro-invertebrate communities in the Galapagos archipelago. Journal of Biogeography 31, 1107–1124.
- Edgar, G.J., Banks, S.A., Brandt, M., Bustamante, R.H., Chiriboga, A., Earle, S., Garske, L., Glynn, P.W., Grove, J.S., Henderson, S., Hickman, C.P., Miller, K.A., Rivera, F., Wellington, G.M., 2010. El Nino, grazers and fisheries interact to greatly elevate extinction risk for Galapagos marine species. Global Change Biology 16, 2876–2890.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Forsterra, G., Galvan, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506, 216-220.

Eschmeyer, W.N., Fricke, R., 2016. Catalog of fishes: Genera, species, references.

Estupiñán-Montaña , C., Cedeño-Figueroa, L., Galván-Magaña, F., 2009. Hábitos alimentarios del tiburón martillo *Sphyrna lewini* (Griffith & Smith, 1834) (Chondrichthyes) en el Pacífico ecuatoriano. *Revista de Biología Marina y Oceanografía* 44, 379-386.

Fenopader, 1989. Carta al gobierno en protesta de aleteo de tiburones. Federación de pescadores artesanales del Ecuador, Puerto Ayora, Galapagos, Ecuador.

Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R., Lotze, H.K., 2010. Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters* 13, 1055-1071.

Fischer, J., Erikstein, K., D'Offay, B., Guggisberg, S., Barone, M., 2012. Review of the implementation of the international plan of action for the conservation and management of sharks, In *FAO Fisheries and Aquaculture Circular No. 1076*. Food and Agriculture Organization of the United Nations, Rome, Italy.

Fisher, R.A., 1918. The Correlation Between Relatives on the Supposition of Mendelian Inheritance. *Philosophical Transactions of the Royal Society of Edinburgh* 52, 399-433.

Freitas, C., 2012. Package 'argosfilter'. Argos locations filter. CRAN.

- Friedlander, A., DeMartini, E., 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Marine Ecology Progress Series* 230, 253-264.
- Friedlander, A., Nowlis, J.S., Sanchez, J.A., Appeldoorn, R., Usseglio, P., McCormick, C., Bejarano, S., Mitchell-Chui, A., 2003. Designing effective marine protected areas in Seaflower Biosphere Reserve, Colombia, based on biological and sociological information. *Conservation Biology* 17, 1769-1784.
- Friedlander, A.M., Zgliczynski, B.J., Ballesteros, E., Aburto-Oropeza, O., Bolaños, A., Sala, E., 2012. The shallow-water fish assemblage of Isla del Coco National Park, Costa Rica: structure and patterns in an isolated, predator-dominated ecosystem. *Journal of Tropical Biology* 60, 321-338.
- Froeschke, J., Stunz, G., Wildhaber, M., 2010. Environmental influences on the occurrence of coastal sharks in estuarine waters. *Marine Ecology Progress Series* 407, 279-292.
- Fu, L.-L., Christensen, E.J., Yamarone Jr., C.A., Lefebvre, M., Menard, Y., Dorrer, M., Escudier, P., 1994. TOPEX/Poseidon mission overview. *Journal of Geophysical Research* 99, 24369 - 24382.
- Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E., Gjerde, K., Bustamante, R., Possingham, H.P., Richardson, A.J., 2009. Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology & Evolution* 24, 360-369.
- Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E., Gjerde, K., Bustamante, R., Possingham, H.P., Richardson, A.J., 2010. Pelagic MPAs: The devil you know. *Trends in Ecology & Evolution* 25, 63-64.

- Geist, D.J., Harpp, K.S., 2009. Galápagos island geology. In, Enciclopedia of Islands. pp. 367-372
- Gerhardinger, L.C., Godoy, E.A.S., Jones, P.J.S., 2009. Local ecological knowledge and the management of marine protected areas in Brazil. *Ocean and Coastal Management* 52, 154-165.
- Gilchrist, G., Mallory, M., Merkel, F., 2005. Can local ecological knowledge contribute to wildlife management? Case studies of migratory birds. *Ecology and Society* 10, 20.
- Gillingham, P.K., Alison, J., Roy, D.B., Fox, R., Thomas, C.D., 2015. High Abundances of Species in Protected Areas in Parts of their Geographic Distributions Colonized during a Recent Period of Climatic Change. *Conservation Letters* 8, 97-106.
- Gilman, E., Clarke, S., Brothers, N., Alfaro-Shigueto, J., Mandelman, J., Mangel, J., Petersen, S., Piovano, S., Thomson, N., Dalzell, P., Donoso, M., Goren, M., Werner, T., 2008. Shark interactions in pelagic longline fisheries. *Marine Policy* 32, 1-18.
- GNPS, 1998. Plan de manejo de la Reserva Marina de Galapagos. Galapagos National Park Service, Puerto Ayora, Galapagos, Ecuador.
- Gobierno del Ecuador, 1986. Decreto Ejecutivo No. 1810-A. Registro Oficial No. 434 del 13 de mayo de 1986, ed. R.O.d.E.O.d.G.d. Ecuador. Gobierno del Ecuador, Quito, Ecuador.
- Gobierno del Ecuador, 1997. Decreto Ejecutivo No. 245. Registro Oficial No. 55 del 30 de abril de 1997, ed. R.O.d.E.O.d.G.d. Ecuador. Gobierno del Ecuador, Quito, Ecuador.
- Gobierno del Ecuador, 1998. Ley Especial de Galapagos, ed. L.N.Ó.d.G.d.E. Registro Oficial del Ecuador No. 278, Quito, Ecuador.
- Gosset, W.S., 1942. "Student's" collected papers. Biometrika Office University College London, London.

- Gregory, R.D., Noble, D.G., Custance, J., 2004. The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. *Ibis* 146, 1-13.
- Griffing, D., Larson, S., Hollander, J., Carpenter, T., Christiansen, J., Doss, C., 2014. Observations on abundance of bluntnose sixgill sharks, *Hexanchus griseus*, in an urban waterway in Puget Sound, 2003-2005. *PLoS One* 9, e87081.
- Grothues, T., 2009. A Review of Acoustic Telemetry Technology and a Perspective on its Diversification Relative to Coastal Tracking Arrays. In: J. Nielsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutcavage, J. Sibert (Eds.), *Tagging and Tracking of Marine Animals with Electronic Devices*. Springer Netherlands, pp. 77-90
- Grove, J., 1985. Influence of the 1982-1983 El Niño event upon the ichthyofauna of the Galápagos Islands. In, *El Niño and the Galapagos Islands: the 1982-83 event*. Charles Darwin Foundation
- Grove, J.S., Lavenberg, R.J., 1998. *The fishes of the Galapagos Islands*. Stanford University Press, California, USA.
- Grubbs, R.D., Carlson, J.K., Romine, J.G., Curtis, T.H., McElroy, W.D., McCandless, C.T., Cotton, C.F., Musick, J.A., 2016. Critical assessment and ramifications of a purported marine trophic cascade. *Scientific Reports* 6, 20970.
- Guisan, A., Edwards Jr, T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling* 157, 89-100.
- Gulak, S.J.B., de Ron Santiago, A.J., Carlson, J.K., 2015. Hooking mortality of scalloped hammerhead *Sphyrna lewini* and great hammerhead *Sphyrna mokarran* sharks caught on bottom longlines. *African Journal of Marine Science* 37, 267-273.



- Halpern, B.S., 2003. The impact of marine reserves: Do reserves work and does reserve size matter? *Ecological Applications* 13, S117-S137.
- Hamilton, W.J., Kennen, E.F.W., 1970. Refuging. *Annual Review of Ecology and Systematics* 1, 263-286.
- Hartog, J., Hobday, A., 2011. SDODE: Spatial Dynamics Ocean Data Explorer. User Guide v3. CSIRO Marine and Atmospheric Research, Hobart, Tasmania, Australia.
- Hartog, J.R., Hobday, A.J., Matear, R., Feng, M., 2011. Habitat overlap between southern bluefin tuna and yellowfin tuna in the east coast longline fishery – implications for present and future spatial management. *Deep Sea Research Part II: Topical Studies in Oceanography* 58, 746-752.
- Hastie, T., Tibshirani, R., 1986. Generalized Additive Models. *Statistical Science* 1, 297-310.
- Hearn, A., Green, J.R., Espinoza, E., Peñaherrera, C., Acuña, D., Klimley, A.P., 2013. Simple criteria to determine detachment point of towed satellite tags provide first evidence of return migrations of whale sharks (*Rhincodon typus*) at the Galapagos Islands, Ecuador. *Animal Biotelemetry* 1, 11.
- Hearn, A., Ketchum, J., Klimley, A.P., Espinoza, E., Penaherrera, C., 2010. Hotspots within hotspots? Hammerhead shark movements around Wolf Island, Galapagos Marine Reserve. *Marine Biology* 157, 1899-1915.
- Hearn, A., Ketchum, J., Shillinger, G., Klimley, A., Espinoza, E., 2008. Programa de Investigación y Conservación de Tiburones en la Reserva Marina de Galápagos. Reporte Anual 2006-7. Charles Darwin Foundation, University of California - Davis and Galapagos National Park, Puerto Ayora, Galapagos, Ecuador.
- Hearn, A.R., Acuña, D., Ketchum, J.T., Peñaherrera, C., Green, J., Marshall, A., Guerrero, M., Shillinger, G., 2014. Elasmobranchs of the Galapagos Marine Reserve. In: J.

- Denkinger, L. Vinuela (Eds.), Galapagos Marine Reserve: a dynamic socio-ecological system. Springer, pp. 23-59
- Heithaus, M.R., 2004. Reproductive biology of elasmobranchs. In: J.C. Carrier, J.A. Musick, M.R. Heithaus (Eds.), Biology of Sharks and Their Relatives. CRC Press, Boca Raton, FL, USA, p. 504
- Heupel, M., Hueter, R., 2002. Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. Marine Freshwater Research 53, 543-550.
- Heupel, M.R., Semmens, J.M., Hobday, A.J., 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening stations arrays. Marine and Freshwater Research 57, 1-13.
- Heupel, M.R., Simpfendorfer, C.A., 2002. Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. Canadian Journal of Fisheries and Aquatic Sciences 59, 624-632.
- Heupel, M.R., Simpfendorfer, C.A., 2005. Quantitative analysis of aggregation behavior in juvenile blacktip sharks. Marine Biology 147, 1239-1249.
- Hickman, C.J., Keen, S., Larson, A., Eisenhour, D., I'Anson, H., Roberts, L., 2013. Integrated Principles of Zoology 16th Edition, 16th Edition edn. McGraw-Hill Education, New York, NY, USA.
- Hobday, A.J., Hartmann, K., 2006. Near real-time spatial management based on habitat predictions for a longline bycatch species. Fisheries Management and Ecology 13, 365-380.
- Hobday, A.J., Hartog, J.R., Spillman, C.M., Alves, O., Hilborn, R., 2011. Seasonal forecasting of tuna habitat for dynamic spatial management. Canadian Journal of Fisheries and Aquatic Sciences 68, 898-911.

- Hobday, A.J., Hartog, J.R., Timmiss, T., Fielding, J., 2010. Dynamic spatial zoning to manage southern bluefin tuna (*Thunnus maccoyii*) capture in a multi-species longline fishery. *Fisheries Oceanography* 19, 243-253.
- Hoggarth, D.D., Abeyasekera, S., Arthur, R.I., Beddington, J.R., Burn, R.W., Halls, A.S., Kirkwood, G.P., McAllister, M., Medley, P., Mees, C.C., Parkes, G.B., Pilling, G.M., Wakeford, R.C., Welcomme, R.L., 2006. Stock assessment for fishery management – A framework guide to the stock assessment tools of the Fisheries Management Science Programme (FMSP), In *FAO Fisheries and Aquaculture Technical Paper No.487*. p. 261. Food and Agricultural Organization, Rome, Italy.
- Hooker, S.K., Cañadas, A., Hyrenbach, K.D., Corrigan, C., Polovina, J.J., Reeves, R.R., 2011. Making protected area networks effective for marine top predators. *Endangered Species Research* 13, 203-218.
- Horne, J.S., Garton, E.O., Krone, S.M., Lewis, J.S., 2007. Analyzing animal movements using Brownian bridges. *Ecology* 88, 2354–2353.
- Houvenaghel, G.T., 1984. Oceanographic setting of the Galápagos Islands. In: R. Perry (Ed.), *Galápagos*. Pergamon Press, Oxford, pp. 43-54
- Howard, A., Widdowson, F., 1996. Traditional knowledge threatens environmental assessment. *Policy Options* 17, 34–36.
- Hsu, H.H., Joung, S.J., Hueter, R.E., Liu, K.M., 2014. Age and growth of the whale shark (*Rhincodon typus*) in the north-western Pacific. *Marine and Freshwater Research* 65, 1145.
- Huntington, H.P., 2000. Using traditional ecological knowledge in science: methods and applications. *Ecological Applications* 10, 1270-1274.
- IATTC, 2010. Annual Report 2010. Inter-American Tropical Tuna Commission, La Jolla, California.

- INP, 1964. Apuntes e informaciones sobre la situación de la producción pesquera ecuatoriana y sus mercados, In Instituto Nacional de Pesca, Boletín Técnico. Guayaquil, Ecuador.
- Jaeger, T.F., 2008. Categorical Data Analysis: Away from ANOVAs (transformation or not) and towards Logit Mixed Models. *Journal of Memory and Language* 59, 434-446.
- Jaenig, M., 2010. Sharks (Selachii) in mangrove-fringed habitats of the Galápagos Marine Reserve (GMR) with implications for management and conservation, In Faculty of Biology & Chemistry. University of Bremen, Bremen, Germany.
- Johannes, R.E., 1998. The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends in Ecology and Evolution* 13, 243 - 246.
- Kaplan, D.M., Chassot, E., Gruss, A., Fonteneau, A., 2010. Pelagic MPAs: the devil is in the details. *Trends in Ecology & Evolution* 25, 62-63; author reply 63-64.
- Keech, M.A., Taras, B.D., Boudreau, T.A., Boertje, R.D., 2014. Black bear population reduction and recovery in western Interior Alaska. *Wildlife Society Bulletin* 38, 71-77.
- Keeney, D.B., Heupel, M.R., Hueter, R.E., Heist, E.J., 2005. Microsatellite and mitochondrial DNA analyses of the genetic structure of blacktip shark (*Carcharhinus limbatus*) nurseries in the northwestern Atlantic, Gulf of Mexico, and Caribbean Sea. *Molecular Ecology* 14, 1911-1923.
- Kendall, W.L., 2001. The Robust Design for capture-recapture studies: Analysis using program MARK., In *Proceedings of the 2nd International Wildlife Management Congress*. pp. 279–282. The Wildlife Society, Bethesda, MD.
- Ketchum, J., 2011. Movement patterns and habitat use of scalloped hammerhead sharks (*Sphyrna lewini*) in the Galapagos Islands: Implications for the design of marine reserves. University of California - Davis, Davis, California, USA.

Ketchum, J.T., Hearn, A., Klimley, A.P., Espinoza, E., Peñaherrera, C., Largier, J.L., 2014a. Seasonal changes in movements and habitat preferences of the scalloped hammerhead shark (*Sphyrna lewini*) while refuging near an oceanic island. *Marine Biology* 161, 755-767.

Ketchum, J.T., Hearn, A., Klimley, A.P., Peñaherrera, C., Espinoza, E., Bessudo, S., Soler, G., Arauz, R., 2014b. Inter-island movements of scalloped hammerhead sharks (*Sphyrna lewini*) and seasonal connectivity in a marine protected area of the eastern tropical Pacific. *Marine Biology*.

Klimley, A., 1987. The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environmental Biology of Fishes* 18, 27-40.

Klimley, A., Cabrera-Mancilla, I., Castillo-Geniz, J., 1993. Horizontal and vertical movements of the scalloped hammerhead shark, *Sphyrna lewini*, in the southern Gulf of California, Mexico. *Ciencias Marinas* 19, 95-115.

Klimley, A., Nelson, D.R., 1984. Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system. *Behavioral Ecology and Sociobiology* 15, 9.

Klimley, A.P., 1983. Social organization of schools of the Scalloped Hammerhead shark, *Sphyrna lewini* (Griffith and Smith), in the Gulf of California, In Scripps Institution of Oceanography Technical Report. University of California, San Diego.

Klimley, A.P., 1985. Schooling in *Sphyrna lewini*, a species with low risk of predation: a non-egalitarian state. *Zeitschrift für Tierpsychologie* 70, 297-319.

Klimley, A.P., Nelson, D.R., 1981. Schooling of scalloped hammerhead, *Sphyrna lewini*, in the Gulf of California. *Fishery Bulletin* 79, 356-360.

Klimley, A.P., Oerding, S., 2013. *The Biology of Sharks and Rays*. University Of Chicago Press, Chicago, Il, USA.

- Krivan, V.V., 1998. Effects of Optimal Antipredator Behavior of Prey on Predator-Prey Dynamics: The Role of Refuges. *Theoretical Population Biology* 53, 131-142.
- Kruskal, W.H., Wallis, W.A., 1952. Use of Ranks in One-Criterion Variance Analysis. *Journal of the American Statistical Association* 47, 583-621.
- Lancaster, H.O., 2004. Chi-Square Distribution. In, *Encyclopedia of Statistical Sciences*. John Wiley & Sons, Inc.
- Lee, K.A., Huveneers, C., Gimenez, O., Peddemors, V., Harcourt, R.G., 2014. To catch or to sight? A comparison of demographic parameter estimates obtained from mark-recapture and mark-resight models. *Biodiversity and Conservation*.
- Lincoln Smith, M.P., 1989. Improving multispecies rocky reef fish censuses by counting different groups of species using different procedures. *Environmental Biology of Fishes* 26, 29-37.
- Llerena, Y., 2009. Identificación de tiburones juveniles y caracterización de sus hábitats en las zonas costeras de pesca de la isla San Cristóbal - Reserva Marina de Galápagos, In *Facultad de Ciencias Naturales. Escuela de Biología.*, p. 77. Universidad de Guayaquil, Guayaquil, Ecuador.
- Llerena, Y., Espinoza, E., Murillo, J.C., 2010. Identification of rearing areas for blacktip sharks *Carcharhinus limbatus* in the mangrove stands of coastal San Cristobal Island. In: D.C. CDF (Ed.), *Galapagos Report 2009-2010*. Puerto Ayora, Galapagos, Ecuador
- Llerena, Y., Peñaherrera, C., Espinoza, E., Hirschfeld, M., Wolff, M., Vinueza, L.R., 2015. Nursery grounds of blacktip sharks (*Carcharhinus limbatus*) in mangrove-fringed bays in the central part of the Galapagos Archipelago. In: L.J. Cayot, D. Cruz, R. Knab (Eds.), *Galapagos Report 2013-2014*. GNPD, GCREG, CDF and GC
- Lloor-Andrade, P., Galván-Magaña, F., Elorriaga-Verplancken, F.R., Polo-Silva, C., Delgado-Huertas, A., 2015. Population and individual foraging patterns of two

hammerhead sharks using carbon and nitrogen stable isotopes. *Rapid Communications in Mass Spectrometry* 29, 821-829.

Lubchenco, J., Gaines, S., Grorud-Colvert, K., Airame, S., Palumbi, S., Warner, R., Simler Smith, B., Alcala, A., Branch, G., Brumbaugh, D., 2007. *The science of marine reserves*, 2nd edn. PISCO, Corvallis, Oregon, USA.

Ludwig, D., Hilborn, R., Walters, C.J., 1993. Uncertainty, resource exploitation and conservation: lessons from history. *Science* 260, 17–20.

Maccherone, B., Frazier, S., 2015. Moderate Resolution Imaging Spectroradiometer (Modis). National Aeronautics and Space Administration (NASA).

Mansur, R.M., Strindberg, S., Smith, B.D., 2012. Mark-resight abundance and survival estimation of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, in the Swatch-of-No-Ground, Bangladesh. *Marine Mammal Science* 28, 561-578.

Martinez-Ortiz, J., Aires-da-Silva, A.M., Lennert-Cody, C.E., Maunder, M.N., 2015. The Ecuadorian artisanal fishery for large pelagics: Species composition and spatio-temporal dynamics. *PLoS One* 10, e0135136.

McClintock, B.T., White, G.C., 2012. From NOREMARK to MARK: software for estimating demographic parameters using mark-resight methodology. *Journal of Ornithology* 152, 641-650.

McClintock, B.T., White, G.C., Antolin, M.F., Tripp, D.W., 2009. Estimating abundance using mark-resight when sampling is with replacement or the number of marked individuals is unknown. *Biometrics* 65, 237-246.

Meffe, G.K., Carroll, C.R., 1997. *Principles of Conservation Biology*, 2nd Edition edn. Sinauer Press, Sunderland, MA, USA.

- Melnychuk, M.C., Walters, C.J., 2010. Estimating detection probabilities of tagged fish migrating past fixed receiver stations using only local information. *Canadian Journal of Fisheries and Aquatic Sciences* 67, 641-658.
- Merlen, G., 1995. Use and misuse of the seas around the Galápagos Archipelago. *Oryx* 29, 99.
- Minta, S., Mangel, M., 1989. A Simple Population Estimate Based on Simulation for Capture-Recapture and Capture-Resight. *Ecology* 70, 1738-1751.
- Mood, A.M., 1954. On the Asymptotic Efficiency of Certain Nonparametric Two-Sample Tests. *The Annals of Mathematical Statistics* 25, 514-522.
- Muhlfeld, C.C., Taper, M.L., Staples, D.F., Shepard, B.B., 2006. Observer Error Structure in Bull Trout Redd Counts in Montana Streams: Implications for Inference on True Redd Numbers. *Transactions of the American Fisheries Society* 135, 643-654.
- Murillo, J., Reyes, H., Zarate, P., Banks, S., Danulat, E., 2004. Evaluación de la captura incidental durante el Plan Piloto de Pesca de Altura con Palangre en la Reserva Marina de Galápagos. Charles Darwin Foundation and Galapagos National Park., Puerto Ayora, Galapagos, Ecuador.
- Myers, R.A., Baum, J., Shepherd, T.D., Powers, S.P., Peterson, C.H., 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315, 1846 - 1850.
- Myers, R.A., Worm, B., 2005. Extinction, survival or recovery of large predatory fishes. *Philos Trans R Soc Lond B Biol Sci* 360, 13-20.
- Neal, A.K., White, G.C., Gill, R.B., Reed, D.F., Olterman, J.H., 1993. Evaluation of mark resight model assumptions for estimating mountain sheep numbers. *The Journal of Wildlife Management* 57, 436-450.



Neis, B., Schneider, D.C., Felt, L., Haedrich, R.L., Fischer, J., Hutchings, J.A., 1999. Fisheries assessment: what can be learned from interviewing resources users? Canadian Journal of Fisheries and Aquatic Sciences 56, 1949-1963.

Norman, B., 2005. *Rhincodon typus*, In The IUCN Red List of Threatened Species. International Union for the Conservation of Nature.

Oeffner, J., Lauder, G.V., 2012. The hydrodynamic function of shark skin and two biomimetic applications. Journal of Experimental Biology 215, 785-795.

Palacios, D.M., 2004. Seasonal patterns of sea-surface temperature and ocean color around the Galapagos: regional and local influences. Deep-Sea Research II 51, 43–57.

Papastamatiou, Y.P., Meyer, C.G., Carvalho, F., Dale, J.J., Hutchinson, M.R., Holland, K.N., 2013. Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator. Ecology 94, 2595-2606.

Pauly, D., 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution 10, 430.

Peñaherrera, C., Hearn, A., 2008. Toward an ecosystem-based approach to fisheries: a risk analysis. In: L.J. Cayot, M.V. Toral-Granda (Eds.), Galapagos Report 2007-2008. Charles Darwin Foundation, Galapagos National Park and Galapagos National Institute, Puerto Ayora, Galapagos Ecuador

Peñaherrera, C., Llerena, Y., Keith, I., 2013. Perceptions of the economic value of sharks for single-day dive tourism and commerce in Santa Cruz Island. In, Galapagos Report 2011-2012. DGNP, GCREG, CDF and GC., Puerto Ayora, Galapagos, Ecuador.

Peñaherrera-Palma, C., Harpp, K., Banks, S., 2013. Rapid seafloor mapping of the northern Galapagos Islands, Darwin and Wolf. Galapagos Research 68, 1-8.

Poizat, G., Baran, E., 1997. Fishermen knowledge in fish ecology quantitative analysis. Environmental Biology of Fishes 50, 435-449.

- Pollock, K.H., 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46, 752–757.
- Pollock, K.H., Jiang, H., Hightower, J.E., 2004. Combining Telemetry and Fisheries Tagging Models to Estimate Fishing and Natural Mortality Rates. *Transactions of the American Fisheries Society* 133, 639-648.
- Priede, I.G., Froese, R., Bailey, D.M., Bergstad, O.A., Collins, M.A., Dyb, J.E., Henriques, C., Jones, E.G., King, N., 2006. The absence of sharks from abyssal regions of the world's oceans. *Proc Biol Sci* 273, 1435-1441.
- Punt, A.E., Walker, T.I., Taylor, B.L., Pribac, F., 2000. Standardization of catch and effort data in a spatially-structured shark fishery. *Fisheries Research* 45, 129-145.
- R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramírez, J., Reyes, H., 2015. Evaluation of the high seas fishery of pelagic fishes in the Galapagos Marine Reserve. In, Galapagos Report 2013-2014. GNPD, GCREG, CDF and GC, Puerto Ayora, Galapagos, Ecuador
- Randall, J., 1977. Contribution to the Biology of the Whitetip Reef Shark (*Triaenodon obesus*). *Pacific Science* 31, 143-164.
- Reilly, S.B., 1990. Seasonal changes in distribution and habitat differences among dolphins in the Eastern Tropical Pacific. *Marine Ecology Progress Series* 66, 1-11.
- Reyes, H., Murillo, J.C., 2007. Efforts to control illegal fishing activities in the Marine Reserve. In: J. Stimson, S. Cardenas, A. Marin (Eds.), Galapagos Report. Puerto Ayora, Galapagos, Ecuador
- Reynolds, R.W., Smith, T.M., Liu, C., Chelton, D.B., Casey, K.S., Schlax, M.G., 2007. Daily High-Resolution-Blended Analyses for Sea Surface Temperature. *Journal of Climate* 20, 5473-5496.

- Rice, C.G., Jenkins, K.J., Chang, W.-Y., 2009. A Sightability Model for Mountain Goats. *Journal of Wildlife Management* 73, 468-478.
- Robbins, W.D., Hisano, M., Connolly, S.R., Choat, J.H., 2006. Ongoing collapse of coral-reef shark populations. *Current Biology* 16, 2314-2319.
- Rochet, M.J., Prigent, M., Bertrand, J.A., Carpentier, A., Coppin, F., Delpech, J.P., Fontenelle, G., Foucher, E., Mahe, K., Rostiaux, E., Trenkel, V.M., 2008. Ecosystem trends: evidence for agreement between fishers' perceptions and scientific information. *ICES Journal of Marine Science* 65, 1057-1068.
- Rohner, C.A., Richardson, A.J., Marshall, A.D., Weeks, S.J., Pierce, S.J., 2011. How large is the world's largest fish? Measuring whale sharks *Rhincodon typus* with laser photogrammetry. *Journal of Fish Biology* 78, 378-385.
- Roman, J., Dunphy-Daly, M.M., Johnston, D.W., Read, A.J., 2015. Lifting baselines to address the consequences of conservation success. *Trends in Ecology and Evolution* 30, 299-302.
- Roman-Verdesoto, M., Orozco-Zoller, M., 2005. Bycatches of sharks in the tuna purse-seine fishery of the Eastern Pacific Ocean reported by observers of the Interamerican Tropical Tuna Commission, 1993-2004, In Data report 11. Inter-American Tropical Tuna Commission, La Jolla, California.
- Ruddle, K., 2000. Systems of Knowledge: Dialogue, Relationships and Process. *Environment, Development and Sustainability* 2, 277-304.
- Ryan, G.E., Dove, V., Trujillo, F., Doherty, P.F., 2011. Irrawaddy dolphin demography in the Mekong River: an application of mark-resight models. *Ecosphere* 2, art58.
- Saenz-Arroyo, A., Roberts, C.M., Torre, J., Carino-Olvera, M., Enriquez-Andrade, R.R., 2005. Rapidly shifting environmental baselines among fishers of the Gulf of California. *Proceedings of the Royal Society B: Biological Sciences* 272, 1957-1962.

- Salazar, S., 2002. Lobo marino y Lobo peletero. In: E. Danulat, G.J. Edgar (Eds.), La Reserva Marina de Galápagos. Línea Base de la Biodiversidad. Fundación Charles Darwin / Parque Nacional Galápagos, Santa Cruz, Galápagos, Ecuador.
- Schacter, D.L., 2002. The seven sins of memory. How the mind forgets and remembers. Houghton Miffling Company, New York, USA.
- Schaeffer, B.A., Morrison, J.M., Kamykowski, D., Feldman, G.C., Xie, L., Liu, Y., Sweet, W., McCulloch, A., Banks, S., 2008. Phytoplankton biomass distribution and identification of productive habitats within the Galapagos Marine Reserve by MODIS, a surface acquisition system and in-situ measurements. *Remote Sensing of Environment* 112, 3044-3054.
- Schiller, L., Alava, J.J., Grove, J., Reck, G., Pauly, D., 2014. The demise of Darwin's fishes: evidence of fishing down and illegal shark finning in the Galapagos Islands. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15, 431-446.
- Seber, G.A., 1982. The estimation of animal abundance and related parameters. Griffin London, London, UK.
- Seber, G.A.F., 1992. A Review of Estimating Animal Abundance II. *International Statistical Review / Revue Internationale de Statistique* 60, 129-166.
- Sequeira, A.M., Mellin, C., Meekan, M.G., Sims, D.W., Bradshaw, C.J., 2013. Inferred global connectivity of whale shark *Rhincodon typus* populations. *Journal of Fish Biology* 82, 367-389.
- Shillinger, G.L., 2005. The Eastern Tropical Pacific Seascape: An innovative model for transboundary marine conservation. In: R.A. Mittermeier, C.F. Kormos, P.R.G. Mittermeier, T. Sandwith, C. Besancon (Eds.), *Transboundary Conservation: A new vision for protected areas*. Conservation International, Washington D.C., USA., pp. 320-331

Shimada, B.M., Shaefer, M.B., 1956. A study of changes in fishing effort, abundance and yield for yellowfin and skipjack tuna in the Eastern Tropical Pacific., In IATTC Bulletins. Inter-American Tropical Tuna Commission, La Jolla, California, United States. .

Shotton, R., 1999. Part 1. Case studies of the management of elasmobranch fisheries, In FAO fisheries technical paper. pp. 1-479, Rome, Italy.

Simpfendorfer, C.A., 1993. Age and growth of the Australian sharpnose shark *Rhizoprionodon taylori* from North Queensland, Australia. Environmental Biology of Fishes 36, 233-241.

Smale, M.J., 2005. *Triaenodon obesus*, In The IUCN Red List of Threatened Species. . p. 2. IUCN 2015.

Smith, S.E., Au, D.W., Show, C., 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. Marine and Freshwater Research 49, 663.

Smith, W.H., 1997. Global Sea Floor Topography from Satellite Altimetry and Ship Depth Soundings. Science 277, 1956-1962.

Snell, H.L., Stone, P.A., Snell, H.L., 1996. A summary of geographic characteristics of the Galápagos Islands. Journal of Biogeography 23, 619–624.

Soler, G.A., Bessudo, S., Guzmán, A., 2013. Long term monitoring of pelagic fishes at Malpelo Island, Colombia. Latin American Journal of Conservation 3, 28-37.

Sollmann, R., Gardner, B., Parsons, A.W., Stocking, J.J., McClintock, B.T., Simons, T.R., Pollock, K.H., O'Connell, A.F., 2012. A spatial mark–resight model augmented with telemetry data. Ecology 94, 553-559.

Soria, M., Dagorn, L., Potin, G., Fréon, P., 2009. First field-based experiment supporting the meeting point hypothesis for schooling in pelagic fish. Animal Behaviour 78, 1441-1446.

- Sorisio, L.S., De Maddalena, A., Visser, I.N., 2006. Interaction between killer whales (*Orcinus orca*) and hammerhead sharks (*Sphyrna sp.*) in Galapagos waters. *Latin American Journal of Aquatic Mammals* 5, 69-71.
- SRP, 1989. Acuerdo Ministerial No. 151, ed. S.-s.d.R. Pesqueros., p. 3. Subsecretaria de Recursos Pesqueros (SRP). Ministerio de Industrias, Ganadería y Pesca, Guayaquil, Ecuador.
- Stevens, J., Bonfil, R., Dulvy, N., Walker, P., 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* 57, 476-494.
- Stewart, J.S., Hazen, E.L., Bograd, S.J., Byrnes, J.E., Foley, D.G., Gilly, W.F., Robison, B.H., Field, J.C., 2014. Combined climate- and prey-mediated range expansion of Humboldt squid (*Dosidicus gigas*), a large marine predator in the California Current System. *Glob Chang Biol* 20, 1832-1843.
- Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, J.E., Baker, S.C., Thomson, R.J., Stuart-Smith, J.F., Hill, N.A., Kininmonth, S.J., Airolidi, L., Becerro, M.A., Campbell, S.J., Dawson, T.P., Navarrete, S.A., Soler, G.A., Strain, E.M., Willis, T.J., Edgar, G.J., 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* 501, 539-542.
- Student, 1908. The probable error of a mean. *Biometrika* 6, 1-25.
- Sutherland, W.J., 1996. *Ecological Census Techniques: A Handbook*, 2nd edition edn. Cambridge University Press., Cambridge, U.K.
- Taylor, R.B., Morrison, M.A., Shears, N.T., 2011. Establishing baselines for recovery in a marine reserve (Poor Knights Islands, New Zealand) using local ecological knowledge. *Biological Conservation* 144, 3038-3046.

- Thompson, P., 2000. *The Voice of the Past: Oral History*, Third edition edn. Oxford University Press, Oxford, UK.
- van Putten, I.E., Frusher, S., Fulton, E.A., Hobday, A.J., Jennings, S.M., Metcalf, S., Pecl, G.T., 2015. Empirical evidence for different cognitive effects in explaining the attribution of marine range shifts to climate change. *ICES Journal of Marine Science*.
- Villegas-Amtmann, S., Costa, D.P., Tremblay, Y., Salazar, S., Aurióles-Gamboa, D., 2008. Multiple foraging strategies in a marine apex predator, the Galapagos sea lion *Zalophus worrebaeki*. *Marine Ecology Progress Series* 363, 299-309.
- Visser, I.N., Bonaccorso, F.J., 2003. New observations and review of killer whale (*Orcinus orca*) sightings in Papua New Guinea waters. *Aquatic Mammals* 29, 150-172.
- Walters, C.J., 1986. *Adaptive management of renewable resources*. MacMillan Pub. Co., New York, NY.
- Ward-Paige, C.A., Keith, D.M., Worm, B., Lotze, H.K., 2012. Recovery potential and conservation options for elasmobranchs. *Journal of Fish Biology* 80, 1844-1869.
- Watson, R.A., Quinn, T.J., 1997. Performance of transect and point count underwater visual census methods. *Ecological Modelling* 104, 103-112.
- Watts, S., Wu, V., 2005. *Tocando Fondo: la desaparición de los tiburones en el Pacífico Tropical Oriental*. WildAid, San Francisco, California, USA.
- Weng, K., O'Sullivan, J., Lowe, C., Winkler, C., Dewar, H., Block, B., 2007. Movements, behavior and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the Eastern Pacific. *Marine Ecology Progress Series* 338, 211-224.
- White, E.R., Myers, M.C., Flemming, J.M., Baum, J.K., 2015. Shifting elasmobranch community assemblage at Cocos Island-an isolated marine protected area. *Conservation Biology*.

- White, G., Garrot, R., 1990. Analysis of wildlife radio-tracking data. Academic Press Inc., San Diego, California, USA.
- White, G.C., Shenk, T.M., 2001. Chapter 13 - Population Estimation with Radio-Marked Animals. In: J.J.M.M. Marzluff (Ed.), Radio Tracking and Animal Populations. Academic Press, San Diego, pp. 329-350
- WildAid, 2010. An analysis of the law enforcement chain in the Eastern Tropical Pacific Seascape. WildAid, San Francisco, California, USA.
- Wolff, M., 2009. Tropical waters and their living resources: ecology, assessment and management. Verlag H. M. Hauschild GmbH, Bremen, Germany.
- Wolff, M., Peñaherrera-Palma, C., Krutwa, A., 2012a. Food web structure of the Galapagos Marine Reserve after a decade of protection: insights from trophic modeling. In: M. Wolff, M. Gardener (Eds.), The role of science for conservation. Routledge, UK.
- Wolff, M., Ruiz, D.J., Taylor, M., 2012b. El Niño induced changes to the Bolivar Channel ecosystem (Galapagos): comparing model simulations with historical biomass time series. Marine Ecology Progress Series 448, 7-22.
- Wood, L.J., Fish, L., Laughren, J., Pauly, D., 2008. Assessing progress towards global marine protection targets: shortfalls in information and action. Oryx 42.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314, 787-790.
- Worm, B., Davis, B., Kettemer, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R., Kessel, S.T., Gruber, S.H., 2013. Global catches, exploitation rates, and rebuilding options for sharks. Marine Policy 40, 194-204.



- Wyrтки, K., Magaard, L., Hager, J., 1976. Eddy energy in the oceans. *Journal of Geophysical Research* 81, 2641-2646.
- Yasué, M., Kaufman, L., Vincent, A.C.J., 2010. Assessing ecological changes in and around marine reserves using community perceptions and biological surveys. *Aquatic Conservation: Marine and Freshwater Ecosystems* 20, 407-418.
- Zar, J.H., 2010. *Biostatistical Analysis*, 5 edn. Prentice Hall, New Jersey, NJ, USA.
- Zarate, P., 2002. Tiburones. In: E. Danulat, G.J. Edgar (Eds.), *La Reserva Marina de Galápagos. Línea Base de la Biodiversidad*. Fundación Charles Darwin / Parque Nacional Galápagos, Santa Cruz, Galápagos, Ecuador., pp. 373-388
- Zeller, D.C., Russ, G.R., 2000. Population estimates and size structure of *Plectropomus leopardus* (Pisces: Serranidae) in relation to no-fishing zones: mark-release-resighting and underwater visual census. *Marine and Freshwater Research* 51, 221.